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A MANUAL

OF

DENTAL ANATOMY

ALSO,

TOMES'
DENTAL SURGERY,
With 289 Illustrations.

Fourth Edition, 16/-.

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A MANUAL
OF
DENTAL ANATOMY
HUMAN AND COMPARATIVE

BY
CHARLES S. TOMES, M.A., F.R.S.

WITH 263 ILLUSTRATIONS

FIFTH EDITION

LONDON
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PREFACE TO THE FIFTH EDITION.

In the following pages it has been my endeavour to give an outline of the more important facts of Odontology, in the hope that it may serve as an introduction to a more extended study of the subject.

Within the last few years great attention has been given to the study of the teeth, and a copious literature has accumulated bearing upon the subject. It has not seemed desirable in a book of this kind to burden the text with many references, neither can they be altogether omitted, and I have, though I fear with by no means consistent results, attempted to give references only to the most important papers, some of which may be regarded as classical, while others deal with controversial subjects not as yet by any means finally settled.

And whilst the rapidly increasing literature has greatly enhanced the labour and difficulty of bringing the book up to date, and of making a judicious selection of that which should be included and that which should be left out, this difficulty has been not a little increased by the fact that the requirements of the different classes of its readers are by no means identical. In the first instance, the book was written largely with a view of providing students working for a qualifying examination in Dental Surgery with a hand-book of a distinctly elementary kind.

But, in the absence of other works of similar scope, it has happened that it is used by students of biology in general, and to meet their requirements it has been necessary to expand those portions which treat of Comparative Odontology.

I take this opportunity of expressing my indebtedness to the Odontographies of Owen and Giebel, to Flower and Lydekker's "Mammalia," to the Article on Teeth by Dr. Wortmann in the "American System of Dental Surgery," and to the rich contributions of Professors Marsh, Cope, and Osborn to our knowledge of the very varied extinct Mammalian Fauna of America.

CHARLES S. TOMES.

9, Park Crescent, London, W.,
March, 1898.

TABLE OF CONTENTS.

CHAPTER I.

PAGE
The Nature of Teeth—The Dental Tissues—Enamel . . . 1

CHAPTER II.

Dentine and its Varieties 38

CHAPTER III.

The Tooth-pulp—Cementum—The Gum—The Alveolo-dental Membrane 86

CHAPTER IV.

The Development of the Teeth in Fish, Reptiles, and Mammals 110

CHAPTER V.

The Calcification of the Dental Tissues—The Eruption of the Teeth and Development of the Jaws 154

CHAPTER VI.

The Attachment of the Teeth by Membrane, by Hinges, by Anchylosis, and by Sockets 222

CHAPTER VII.

The Teeth of Fishes 236

CHAPTER VIII.

The Teeth of Batrachia, Reptiles, and Birds 265

CHAPTER IX.

PAGE
THE TEETH OF MAMMALS—THE PROTOTHERIA AND THE ARRANGEMENT OF THE EUTHERIA 298

CHAPTER X.

THE TEETH OF EUTHERIA—INTRODUCTORY REMARKS—TRITUBERCULISM—THE GENESIS OF TOOTH FORMS 308

CHAPTER XI.

THE HOMOLOGIES OF THE TEETH — THE MILK DENTITION — THE TEETH OF EDENTATA, CETACEA, AND SIRENIA—THE TEETH OF UNGULATA 347

CHAPTER XII.

THE TEETH OF PROBOSCIDEA, DINOCERATA, RODENTIA, CARNIVORA . 424

CHAPTER XIII.

THE TEETH OF INSECTIVORA AND CHIROPTERA 480

CHAPTER XIV.

THE TEETH OF PRIMATES—THE TEETH OF MAN 500

CHAPTER XV.

THE MAXILLARY BONES—THE NERVES OF THE TEETH 545

CHAPTER XVI.

THE TEETH OF MARSUPIALS 562

APPENDIX 585

A

MANUAL OF DENTAL ANATOMY

HUMAN AND COMPARATIVE.

CHAPTER I.

THE DENTAL TISSUES.

THE range of the subject of Dental Anatomy turns upon the meaning which is attached to the word "Tooth;" but, although this chapter might most appropriately open with a definition of this word, it is very much easier to explain what is ordinarily understood by it, than to frame any single sentence which shall fulfil the requirements of logical definition. Most vertebrate and a great many invertebrate animals have certain hard masses in or near to the orifice of the alimentary canal, *i.e.*, the mouth; by these hard masses, sometimes of bony and sometimes of horny nature, various offices in connection with the prehension or comminution of food are performed, and to them the term "teeth" is applied. But whilst in some animals these functions are performed by horny bodies, recent researches have shown that, at all events in several cases, these horny teeth are superimposed upon true tooth germs, calcified to some extent, which they supersede, and the exact relation of the one to the other requires further elucidation. In many animals, teeth have come to be used for purposes other than those of nutrition, such as for sexual warfare; but it can hardly be doubted that teeth primarily had to do with the nourishment of their possessor.

The subject of the homologies of the teeth cannot be fully entered upon until the details of their development have been mastered; still, a few words may even at the outset be devoted to the elucidation of their real nature.

The mucous membrane which lines the alimentary canal is continuous with—is, indeed, a part of—the external skin, with which it blends at the lips. Now, if a young dog-fish, just about to be hatched, be examined, it will be found that it has no distinct under lip, but that its skin turns in over its rounded jaw without interruption. The skin outside carries spines (placoid scales) (¹), and these spines are continued over that part of it which enters the mouth and bends over the jaws; only they are a little larger in this latter position.

It may occur to the reader that it is a remarkable thing that the skin and its associated structures should be found in the mouth at all, but a very easy explanation is afforded by the facts of embryology. At the stage immediately prior to the appearance of the embryo, the egg is enveloped by cells which are differentiated into two layers; then, in the neighbourhood where the embryo is about to appear, a third layer is separated off, which lies between the other two, and is derived mainly, perhaps according to some observers wholly, from the outer layer.

These three layers are called the epiblast, the mesoblast, and the hypoblast.

From the epiblast are ultimately formed the enamel of the teeth, the epithelium of the mouth (with the exception of that which covers the tongue and the back part of the floor of the mouth), the skin and its appendages, such as hair and nails, the epithelium of skin, glands, and a variety of other structures, such as the nervous system, with which we have no present concern.

From the mesoblast are formed the dentine and cementum, the skeleton, and all the connective tissues of the body, the muscular system, &c., &c.

From the hypoblast are formed the epithelium of the whole alimentary canal, from the back of the mouth to the anus, and a number of other internal epithelia.

Now, as the embryo begins to take definite shape, that which is going to be its intestinal tract is for a long time widely open into the general interior cavity of the egg or yelk sac, but the embryo grows forwards and backwards in such a way as to form blind

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(¹) "The placoid scale has the structure of dentine; is covered by enamel, and is continued at its base into a plate formed of osseous tissue." Gegenbaur's "Comparative Anatomy," translated by F. Jeffery Bell, p. 424.

pouches at each end, in the one case in front and in the other behind, but still in communication with the cavity of the yelk; and were this state of things to be perpetuated while the alimentary canal becomes gradually pinched off and finally closed from the yelk sac, there would be neither mouth nor anus, but it would terminate in blind extremities near either end of the embryo. At the hinder end this sometimes happens, and the result is that the child is born with an imperforate anus.

At this stage the parts are named the foregut (the blind anterior end), the midgut, and the hindgut. The mouth is formed later by an invagination of the surface, so as to make a pouch (stomodœum) reaching down to the foregut, but it is still some time before the septum between them breaks down. The anus is formed in a similar way, the invagination (proctodœum) being much shallower and occurring at a later date.

Thus we have in the mouth a portion of the actual exterior, or future skin, of the embryo carried in, and so it ceases to be a matter for surprise that we should find in the mouth skin structures, viz., dermal spines.

It is, however, pointed out by Dr Wortman ("American System of Dental Surgery," 1887), on the authority of Mr. Ryder, that the teeth of those fish which have teeth upon the gill arches and pharyngeal bones, lie beyond the limits of the invaginated integument, and are therefore of hypoblastic derivation. He goes on to add that, if this be true, the generalisation that all teeth are modified dermal spines is certainly incorrect. It affords us, however, in that case, an example in which identical structures have been produced from tissue of vastly different origin in a similar manner, and in all probability attributable to the same cause, viz., repeated stimulation of a particular point, which eventually gave rise to a calcified papilla.

If the growth of the dog-fish be followed, those spines of the skin which cover the jaws become developed to a far greater size than those outside, a groove without spines appears between the jaw and the lip, and the identity and continuity of the two become to some extent masked. No one can doubt, whether from the comparison of adult forms or from a study of the development of the parts, that the teeth of the shark correspond to the teeth of other fish, and these again to those of reptiles and mammals; it may be clearly demonstrated that the teeth of the shark are nothing more than highly developed spines of the skin, and therefore we infer that all teeth bear a similar relation to the skin. This is what is meant when teeth are called "dermal appendages," and are said to be perfectly distinct from the internal bony skeleton of the animal; the teeth of the shark (and of many other creatures) are not only developed, but always remain imbedded in tough mucous membrane, and never acquire any connection with the bone. Indeed, all teeth alike are developed from a part of the mucous membrane, and any connection which they may ultimately get with the bone is a secondary matter. As it has been well expressed by Dr. Harrison Allen ("Anatomy of the Facial Region"), "if the hairs of the scalp were to be inserted into the skull, or of the moustache into the upper jaw, we should express great astonishment, yet such an extreme proposition is no more remarkable than what is seen to take place in the jaws;" again, "the feathers of certain birds making impressions on the radius, the whalebone pendent from the roof of the mouth, are examples of this same association of tegumentary appendages with the bones."

To these examples may be added the horny plates of the Ornithorhyncus, which are pure hardenings of the stratum corneum of the oral epithelium, but nevertheless have definite beds provided for them on the bones.

In their simpler forms, then, teeth are met with as very numerous spines, differing but little from the spines of the skin except in size, and still less from one another. Indeed, if we take the spines of the skin where, as happens in many cartilaginous fish, some are developed to an especially large size for protective purposes, we shall often find them absolutely indistinguishable from teeth upon the jaws, so far as minute structure and general form go, though they may perhaps exceed the teeth in size.

Mr. Nickerson (Bull Museum, Comp. Zool., Harvard, 1893) has minutely investigated the development of the scales of Lepidosteus, which, at all events at an early period, carry upon them small spines. He regards these spines alone as being homologous with the scales of the sharks, the whole scale of lepidosteus then representing the fusion of a number of placoid scales, and consisting, with the exception of these little spines, of their basal portions only. But what is very curious in their development is that, although by the increase of the dermis in the neighbourhood, a sort of papilliform eminence projecting up into the epidermis is formed, the calcification of the scale takes place, not at the line of junction of the two, but well in the substance of the dermis, of which a thick layer of cells intervenes between the epithelium and the outer surface of the forming plate.

Nevertheless, there seems to be a very rudimentary enamel formation upon the tips of the spines; the outer hard layer of these scales, often called ganoin, is in no sense related to enamel, but is a mesoblastic product.

In the next stage, exemplified in many fish, the teeth, though more specialised, are scattered over almost every one of the numerous bones which form part of the walls of the mouth and pharynx; then in reptiles they are much more restricted in position, whilst in mammals they are absolutely confined to the intermaxillary, maxillary, and mandibular (lower maxillary) bones. In fish and reptiles it is the exception for the teeth in different parts of the mouth to differ markedly from each other; in mammals is the rule.

Teeth owe their hardness to an impregnation with salts of lime; the organic matrix may be of albuminoid character, in which case the tooth is of horny consistence, and is spoken of as "cornified;" or the matrix may be, like that of bone, gelatigenous, that is to say, not gelatine, but collagen, the anhydride of gelatine, which passes into gelatine after prolonged boiling; in this case the tooth is more richly impregnated with salts, and is spoken of as "calcified."

Horny teeth, so far as they have been investigated, consist of aggregations of cells of the stratum corneum of the oral epithelium, and they are penetrated on their under side by the papillæ, whose enormously exaggerated epithelial coats have built them up.

The great mass of a calcified tooth is usually made up of "dentine," which gives to it its characteristic form, and often practically constitutes the whole tooth; to this may or may not be added enamel and cementum.

The simplest teeth are hollow cones, and have no roots; they are calcifications of papillæ, and, as has already been mentioned, are sometimes practically identical in structure and form with similar spines upon the skin.

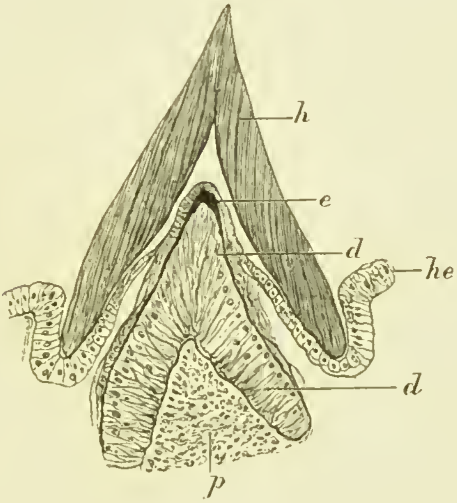
As these simple teeth are generally very numerous, it has occurred to some morphologists that multicuspid teeth have originated by the coalescence of several simple cones, each cusp thus being the representative of an original separate tooth. But there is a good deal to be said against the acceptance of such a view; the question can, however, be better discussed at a subsequent page. So it will suffice to say here that it is much more probable that additional cusps arise by some process of evolution.

It is thus usual to speak of there being two kinds of teeth, namely, horny or albuminous, and calcified teeth; but the development of the former is not yet fully known, and it is hence impossible to determine the exact relation in which they really stand to other, or calcified, teeth.

The horny teeth of Ornithorhyncus have been shown to be purely epithelial, and to consist entirely of cells of the stratum corneum arranged in parallel columns, which are penetrated by papillary processes of the oral mucous membrane. In other words, they are an aggregation of long papillæ, in which the stratum corneum is abundant and hard, squeezed together so as to form a coherent mass. These horny teeth do the work of mastication during the greater part of the animal's life, but until the creature was half grown, it possessed true teeth with multicuspid grinding surfaces and short stunted roots. At that period the horny plates were not fully formed, but they were situated underneath the true teeth, for which they formed a bed, and were incomplete only where the roots of the teeth passed through them. When the teeth were shed they became complete, and the peculiar sculpturing of their surfaces is due to their having once formed a bed for the short-rooted molars. But they were obviously not in any way homologous with true teeth.

The horny teeth which surround the sucking mouth of the lamprey are found to consist of one or more superimposed horny cones, standing upon dermal papillæ, and arising from a horn-producing groove around the base of the papilla (Beard, "Morphological Studies," Jena, 1889). But the horny tooth of Myxine (the hag) is yet more remarkable: in it the horny cone is superimposed, not upon a simple papilla, but upon a tooth germ which goes on to a considerable degree of calcification. Like the horny cone of the lamprey, its free edges rest in a horn-forming groove of oral epithelium. Inside it is a hard cone which appears to be a form of imperfect dentine (with vascular canals in it?): this Dr. Beard believes to be capped with enamel in one of his specimens, and in its interior is a pulp with odontoblasts. There is great difficulty in making out the structure, as these combined horny and calcified teeth almost defy ordinary methods of preparation and section cutting.

Fig. 1 (¹).



The figure given above is somewhat diagrammatic, and is compounded from Dr. Beard's figures, and from a section which he was so kind as to lend me.

Between the horny cap and the dentine is an epithelial structure which is in the position, and seems to play the part of, an enamel organ.

(¹) Tooth of myxine. *d.* Dentine cap. *e.* Enamel (?). *he.* Horn-forming epithelium. *p.* Pulp.

Calcified teeth are composed of one or more structures which are in great measure peculiar to the teeth (although what is to all intents and purposes dentine, is to be found in the skeletons and in the dermal appendages of some fish, and other exceptions might be found to the absolute accuracy of the statement), and hence are called "dental tissues." Notwithstanding the existence of certain transitional forms, it is not possible to doubt the propriety of a general division of dental tissues into three, viz., Dentine, Enamel, and Cementum.

The first named of these constitutes the greater part of all teeth, and so far predominates in mass over the other constituents that, in very many cases, the tooth would nearly retain its form and character after the removal of enamel and cementum.

This central body of dentine, enclosing the pulp, is very often covered by a cap of enamel, which forms the surface of the tooth; this may be very partial, as in the eel or the newt, in which animals only this enamel-capped tip of the tooth projects much above the surface of the mucous membrane; or it may cover a much larger proportion of the tooth, as in man. Perhaps the most usual condition is that the enamel invests the whole crown of the tooth, stopping short at about the level to which the gum reaches, as in the human and most other mammalian teeth of limited growth. In teeth of persistent growth the enamel extends down into the socket as far as the base of the tooth; in such cases it may embrace the whole circumference of the dentine, as in the molar teeth of many rodents, or it may be confined to one side only, as in their incisor teeth, where by its greater hardness it serves to constantly preserve a sharp edge as the tooth is worn away. The enamel is believed to be quite absent from many teeth; thus the order Edentata, comprising sloths, armadillos, and ant-eaters, have it not; the narwal, certain cetaceans, some reptiles, and many fish have none.

But although it might appear an exceedingly simple matter to determine whether a tooth is or is not coated with enamel, as a matter of fact in practice it is not always easy to be certain upon this point. When the enamel is tolerably thick there is no difficulty in making sections which show it satisfactorily, but when it is very thin it is apt to break off in grinding down the section. And even when it does not, it is in such cases usually quite transparent and structureless, and the outermost layer of the dentine being also clear and structureless, it is very hard to decide whether the appearance of a double boundary line is a mere optical effect due to the thickness of the section, or is indicative of a thin layer of a distinct tissue, which again might be either enamel or cementum, for very thin layers of cementum also look very much like enamel.

My own investigations upon the development of the teeth of fish and reptiles have led me to suspect that rudimentary layers of enamel exist upon many teeth on which their presence has not been recognised, for I have found that the formative enamel organs occur universally, at least they exist upon all tooth germs which have been adequately examined. Upon the teeth of snakes, which were stated by Professor Owen to be composed only of dentine and cement, I have endeavoured to show that a thin layer of enamel exists, and that there is no cementum. The frog has an enamel organ as distinct as that of the snake, but I am hardly positive that there is enamel upon its teeth, although there is an appearance of a thin coat of distinct tissue. I have also demonstrated that the armadillo has an enamel organ, but have failed to discover any enamel or anything like it upon the adult teeth, and Professor Sir Wm. Turner has made a similar observation upon the narwal.

At all events we may safely say that in these and many other creatures no functional development of enamel takes place: whether it does or does not exist in an extremely thin and rudimentary layer has become a question of much less significance, since I have shown the presence of an enamel organ to be universal at an early stage.

Hence one may hesitate to endorse Sir Richard Owen's generalisation that the dentine is the most and enamel the least constant of dental tissues; it is to be remembered that it may be so in completed teeth, but recent researches into the development of teeth have very materially modified the conceptions formed as to the relations of the dental tissues to one another, and must lead us to examine carefully such deductive statements before accepting them.

The remaining dental tissue is cementum, which clothes, in a layer of appreciable thickness, the roots of mammalian teeth, and reaches up as far as the enamel, the edge of which it overlaps to a slight extent, or even entirely covers, so that when the cementum is present upon the crown, it occupies a position external to that of the enamel. Cementum occurs universally upon the teeth of mammalia, but it is not always confined to the root of the tooth; in many teeth of persistent growth it originally invested the whole crown, and after it has been worn from the exposed grinding surface, continues to invest the sides of the tooth. (See the description of the complex teeth of the elephant, cow, horse, &c.)

It is probably entirely absent from the teeth of snakes, and indeed of very many reptiles; in the reptilian class, at all events, it appears to me to be confined to those in which the teeth are lodged either in sockets or in a deep bony groove, as I am unacquainted with any tooth anchylosed to the jaw in which it exists, unless we are inclined to include under the term cementum the tissue which I have designated "bone of attachment." (See "Implantation of Teeth.")

ENAMEL.

Upon the outer surface of the dentine the enamel forms a cap of a very much harder and denser material. In its most perfect forms it is very far the hardest of all tissues met with in the animal body, and at the same time the poorest in organic matter. It has been usual to suppose that in the enamel of a human adult tooth there is as little as 3½ to 5 per cent. of organic matter; the lime salts consist of a large quantity of calcium phosphate, some carbonate, and a trace of fluoride; in addition, there is a little magnesium phosphate.

Von Bibra gives two analyses of enamel:

	ADULT MAN.	ADULT WOMAN.
Calcium Phosphate and Fluoride	89·82	81·63
Calcium Carbonate	4·37	8·88
Magnesium Phosphate	1·34	2·55
Other Salts	·88	·97
Cartilage	3·39	5·97
Fat	·20	a trace
Organic	3·59	5·97
Inorganic	96·41	94·03

Hoppe Seyler, who believes that the salt mainly present in bone, dentine, and enamel is a compound salt, in which three molecules of calcium phosphate are combined with one of calcium carbonate, $CA_{10}\ CO_3\ (PO_4)_6$ (just as in the mineral apatite two molecules of fluorine are combined with three of calcium phosphate), gives as his analysis:

$CA_{10}\ \dot{C}O_3\ (PO_4)_6$	95·35
$Mg.\ HPO_4$	1·05
Organic substance	3·60

A large number of other analyses have been from time to time published, in which the proportion of organic matter ranges from two to seven or eight per cent.

I myself undertook a series of experiments with, at first, the object of ascertaining what the nature of this organic matter was ("Journal of Physiology, 1896"), but I failed to discover, in any notable quantity, any substance giving proteid or proteoid reactions.

It is expressly stated in setting out some of the published analyses that the organic matter was estimated simply by the loss on ignition, and this appears to have been the case in all, for in none of them is water set down as a constituent of dried enamel.

But my own analyses showed that, in the case of elephant's enamel, which was selected because it was, from its thickness, comparatively easy to get it tolerably free from adherent fragments of dentine or cementum, there was as much as four per cent. of water left after the enamel had been long dried at a temperature of 300° F.; this water, which was apparently held in somewhat close chemical combination, was, under ignition, given off suddenly, and with such violence as to cause the fragments of enamel to crepitate and fly to pieces, and it was possible to collect it in a chloride of calcium tube and to weigh it, so as to prove that the total loss on ignition was very nearly accounted for by the water given off.

It would be out of place to repeat here in detail all the experiments which led me to my conclusions, as they are to be found in the paper referred to; it will suffice to say that I was able to completely satisfy myself that there is no organic matter at all (in any noteworthy amount) in enamel, and that that which has heretofore been set down as organic matter is simply water combined with the lime salts.

When fragments of enamel are ignited in a hard glass tube, it is seen that the surfaces which had lain in contact with dentine or cementum blacken, but that fractured surfaces in the midst of the enamel do not blacken at all but remain snowy white; it is thus shown that the very minute traces of organic matter found are mainly due to the practical impossibility of getting enamel quite free from adherent dentine or cementum, a conclusion confirmed by the microscopic examination of the trifling residue left when such enamel is dissolved in acids.

As a check experiment a solution was prepared which contained one quarter per cent. of dissolved dentine matrix, and this was added to a solution of enamel salts; this gave abundant proteid reactions. And it has long been a familiar fact that enamel treated with acid on a slide disappears, whereas the organic matter in the prismatic layer of the shell of the mollusc Pinna, which bears a superficial resemblance to enamel, retains its structure and is actually more bulky than before decalcification, although it only amounts to 1·3 per cent. of the weight of the shell employed.

Enamel is then to be regarded as an inorganic substance composed of lime salts which have been deposited in particular patterns and formed under the influence of organic tissues, which have themselves disappeared during its formation.

A very minute trace of organic matter was perhaps sometimes to be extracted by maceration of powdered enamel in caustic potash or baryta water, the addition of acetic acid producing a cloudiness; the quantity obtainable is far too small for identification, but the reaction above mentioned would indicate that it was either mucin or nucleo-albumin; it might have been derived from the fluids of the mouth, and in any case is in too small amount to be of much significance.

The prisms of enamel, obtained by scraping or crushing young enamel, hardly undergo any alteration in form or appearance by ignition; they, however, perhaps become a little more granular, and this slight amount of the alteration seems to go to confirm what has already been said as to the absence of organic matter, as the expulsion of the combined water might easily cause a slight difference in the appearance of the crystalline salts.

The water is probably combined with the calcium phosphate; tribasic calcium phosphate when prepared by any wet method retains in combination one or more equivalents of water, which it will not part with below red heat, and my analyses show the presence of water in about (though not absolutely exactly) the proportion of one equivalent. It may be from this slight discrepancy, there being a little too much water, that enamel is from its physical structure very difficult to dry absolutely, or perhaps some of the calcium phosphate retains two and the rest only one equivalent of water.

Enamel is of very common occurrence in the teeth of fish, reptiles, and mammalia, and is also to be found upon many dermal scales in fish; this is only what was to be expected, as the occurrence of an enamel organ in early development is absolutely universal.

But it varies in amount, forming sometimes a complete coat, sometimes a very partial investment, sometimes a mere spear point to give sharpness to the tooth, and sometimes it appears to be wholly absent.

In teeth of limited growth it terminates at the neck of the tooth, where it is slightly overlapped by the cementum; and where there is a complete coat of cementum over the crown this lies outside the enamel, which is then between the cementum and the dentine.

The cap of enamel on a human tooth is of varying thickness, being thicker in the neighbourhood of the cusps than elsewhere.

Its outer surface is often finely striated, the striæ being transverse to the long axis of the crown; in addition to this fine striation there may be a few deeper and more pronounced grooves, or pits, which are pathological, and are marks of checks in development more or less complete. The enamel of some animals is, to all appearance, structureless; such is the nature of the little caps which, like spear points, surmount the teeth of some fishes and which from their extreme brittleness are often lost in preparing sections, so that their very existence has long been overlooked. Some of these enamel tips, however, present an appearance somewhat similar to the enamel of Sargus (p. 36). But the absence of structure, if such it really be, is after all a mere question of degree: in the commonest form of enamel, such as that of the human teeth, there is a finely prismatic structure, very apparent in imperfect teeth, but far less so in well-formed ones, and the enamel tips of fish are, in the manner of their development, prismatic; so that even though we cannot distinguish its constituent prisms when it is completed, this is merely an indication that calcification has progressed a little farther than in human teeth: if calcification only goes far enough, all structure, if not destroyed, might at all events be masked from sight.

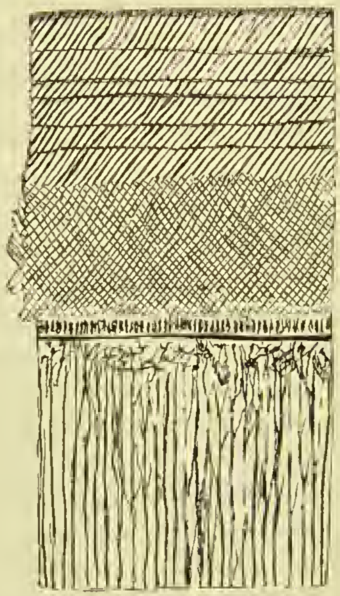
The structure of human enamel has been stated to be fibrous; that is to say, it has a cleavage in a definite direction, and is capable of being broken up into fibres or prisms, which seem in transverse section to approximate more or less closely to hexagonal forms brought about by their mutual apposition. The prisms run from the dentine towards the free surface, their course being subject to many minor modifications. The curved and decussating course of the human enamel prisms renders it difficult to trace them throughout their length, but the structure of the enamel of many lower animals (especially the rodents) is more easily intelligible. Enamel such as that of the Manatee, in which all the prisms pursue a perfectly straight course, is of comparatively rare occurrence, but among the rodents the courses pursued by the enamel prisms are simple, and produce very regular patterns, which are constant for particular families (J. Tomes). Thus, in the *Sciuridæ*, a section of the enamel, whether longitudinal or transverse to the axis of the tooth, appears divided into outer and inner portions, in which the prisms, although continuous from the dentine to the free surface, pursue different directions. As seen in longitudinal section, the enamel prisms start from the dentine at right angles to its surface, and after passing through about two-thirds of the thickness of the enamel in this direction, abruptly bend upwards, forming an angle of 45 degrees with their original course. In transverse section the enamel prisms are found to be arranged in horizontal layers, each layer being a single prism in thickness; in alternate layers the prisms pass to the right and to the left, crossing those of the next layer at right angles, and thus making a pattern of squares in the inner two-thirds of the enamel. But in the outer third of the enamel, where the prisms bend abruptly upwards, those of superimposed layers no longer pass in opposite directions, but are all parallel; in fact no longer admit of distinction into alternate laminæ.

Thus each layer of enamel prisms passes in a very definite direction and, seen with those of other layers, forms a very characteristic pattern; but the enamel prisms are not in any part of their course curved.

In the beaver the course of the prisms is not quite so simple: to take the longitudinal section first, instead of the prisms starting off at right angles to the surface of the dentine, they are inclined upwards towards the apex of the tooth at an angle of 60 degrees; then, after passing through about half the thickness of the enamel, they turn up abruptly again, so that they are approaching to parallelism with the dentine, here making in fact an angle a little less than 30 degrees with it.

It follows from this that no transverse section can show very plainly the direction of the prisms in both parts of their course. The most instructive transverse section is one cut parallel with the layers near to the dentine; this will plainly show the successive layers passing to the right and to the left just as in the squirrel, but the yet more inclined fibres of the outer half of the enamel will then be cut across obliquely; and the figure may be regarded as

Fig. 2 (¹).

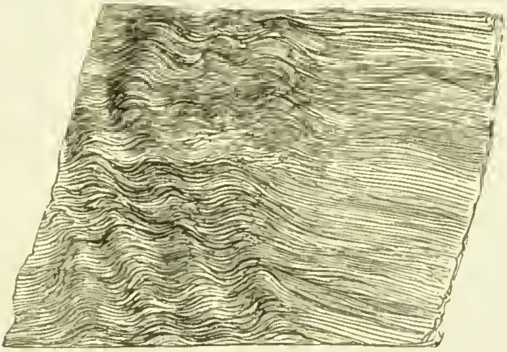


(¹) Transverse section of dentine and enamel of a left lower incisor of a beaver; in the inner half the prisms of contiguous layers cross each other at right angles, in the outer they are parallel.

It is obvious that a transverse section, in order to show the decussation of superimposed layers clearly, must be parallel with the layers, *i.e.*, oblique to the axis of the tooth. But this obliquity will not be right for the outer portion in which the fibres are yet more inclined upwards, so that in it several layers will be cut across somewhat obliquely.

so far diagrammatic that this obliquity of cutting has been corrected in representing the dentinal tubes, whilst the lines parallel with the surface represent the outcrop of successive layers of enamel prisms. It is still further complicated by the fact that the outer layers are not only inclined upwards but also sideways towards the middle line of the head : thus the middle line of the head would be to the right of the section as represented. As regards the decussation of the prisms of alternate layers, it is similar to that of the *Sciuridæ*, but it differs in the laminæ being slightly flexuous instead of pursuing perfectly straight lines.

FIG. 3 (¹).



In the porcupine family very much more complex patterns are met with, the enamel prisms being individually flexuous, and their curves not being confined to one plane; the individual prisms pursue a serpentine course, and cannot be followed far in any one section. Near to the surface, however, they all become parallel, the enamel thus conforming with that of other rodents in being divided into two portions (at least so far as the course pursued, and the pattern traced by its fibres in its inner and outer parts can be said to so divide it). The *Leporidæ*, or hares, form an exception; their enamel has no such lamelliform arrangement, but is built up merely of slightly flexuous prisms.

(¹) Human enamel, from the masticating surface of a molar. The figure is merely intended to show the general direction of the fibres.

By tracing the courses of enamel prisms from the simple pattern found in the manatee through that of the squirrel, dormouse, and the porcupine, we see how a very definite arrangement, at first simple, becomes modified into something a little more complex, till at last it reaches a degree of complexity that looks like mere disorder. No one unfamiliar with the enamel of other rodents, looking at the enamel of the porcupine, would be able to unravel the very indefinite looking chaos of prisms before him ; but had he studied forms in some degree transitional he could not doubt that the tortuous, curving course which he saw the prism to be pursuing was nevertheless perfectly definite and precise, and formed part of a regular pattern.

It is very usual for the individual prisms in enamels, like dentinal tubes, to pursue a spiral course.

In perfectly healthy human enamel the fibrillar arrangement is not so very strongly marked ; the prisms are solid, are apparently in almost absolute contact with one another, without much visible intervening substance.

But Bödecker, basing his conclusions upon the examination of thin sections stained with chloride of gold, holds that enamel is built up of columns of calcified substance, between which minute spaces exist. These are filled by a material which takes the stain deeply, and is probably analogous to the cement substance of epithelial formations. He states that it gives off exceeding fine thorns, which apparently pierce the prisms at right angles to their length, so that it forms a close network very intimately mixed up with the calcified portion of the enamel.

It is not of uniform thickness, but is beaded, and Bödecker attributes to it a rôle of far greater importance than that of a mere cementing substance, for he regards it as being an active, protoplasmic network, which renders the enamel much more "alive" than it had hitherto been considered to be. He believes it to become continuous with the soft contents of the dentinal tubes through the medium of large masses of protoplasmic matter, which he believes he found at the margins of the enamel and dentine.

Klein remarks that "the enamel cells, like all epithelial cells, being separated from one another by a homogeneous interstitial substance, it is clear that the remains of this substance must occur also between the enamel prisms; in the enamel of a developing tooth the interstitial substance is larger in amount than in the fully formed organ. It is improbable that nucleated protoplasmic masses are contained in the interstitial substance of the enamel of a fully formed tooth, as is maintained quite recently by Bödecker."

Von Ebner, who has recently investigated the subject of enamel ("Sitzungsberichte d. Kaiser: Akad.," 1889), holds that there is an uncalcified cement substance between the prisms, which appears to be traceable into continuity with Nasmyth's membrane, which latter, however, acids cause to peel off, so that this continuity may be merely apparent.

Bödecker's views have, however, never obtained much credence, and the result of Mr. Leon Williams's observations and of my own analyses seem to completely dispose of them, as also of those of von Ebner, the appearances being explicable without the assumption of the presence of a noteworthy amount of organic matter. Many stains, and notably chloride of gold, will stain crevices even in mineral specimens, so that too much reliance must never be placed on its results alone.

On the whole the prisms are parallel, and run from the surface of the dentine continuously to that of the enamel. Their paths are not, however, either perfectly straight or perfectly parallel, for alternate layers appear to be inclined in opposite directions, while they are also wavy, forming several curves in their length. The curvature of the enamel prisms is most marked upon the masticating surface; while the layers, alternating in the direction of their inclination as just described, are in planes transverse to the long axis of the crown, and correspond to the fine striæ on the surface of the enamel, which appear to be caused by their outcrop. The curvatures take place in more than one plane; in other words, the course of the individual prism is more or less a spiral.

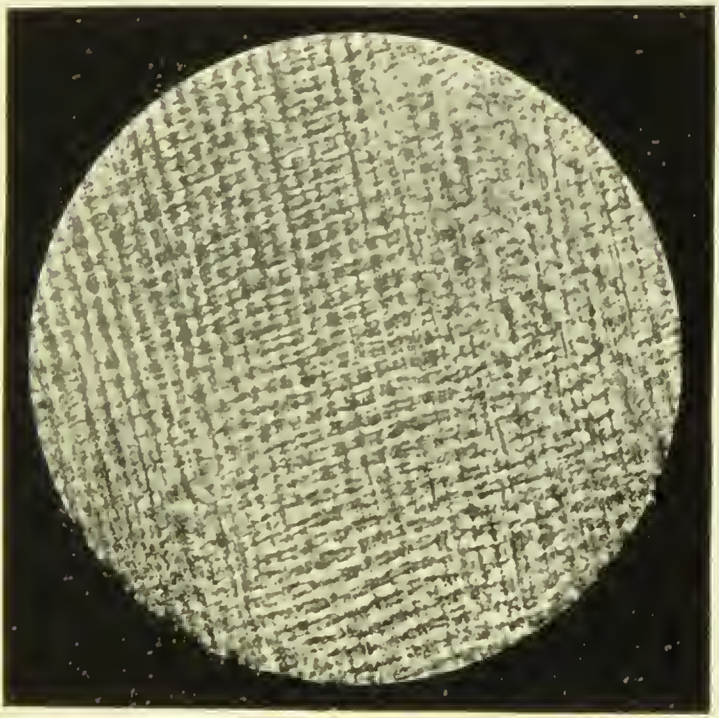
Although most prisms run through the whole thickness of the enamel, yet inasmuch as the area of the outer is much larger than that of the inner surface of the enamel, and the individual prisms do not undergo any alteration in size as they pass outwards, many supplemental fibres are present in the outer portions which do not penetrate far inwards.

The individual prisms are, under a low power, to all appearance structureless in perfectly formed human enamel, but a faint transverse striation, fainter, but otherwise not unlike that of voluntary muscle, is so general that it cannot be regarded as pathological, although it is most strongly developed in imperfect brownish enamel. The striation in question may be seen even in a single isolated prism, and is not necessarily continuous over adjacent prisms, though it generally is so; it is rendered more apparent by the slight action of diluted acids upon the prism. Very various interpretations of this appearance have been given. It has been attributed to "an intermittent calcification" of the enamel prism (Hertz), but was with more probability referred to varicosities in the individual prisms (Kölliker, Waldeyer) (1). It is very marked in the enamel of the common rat, which shares with that of other muridæ the peculiarity of having the individual prisms almost serrated, those of adjacent crossing layers being fitted to one another with great exactness. In human enamel the adjacent prisms if united without any intermediate cementing medium, and pursuing courses slightly different, must of necessity be of slightly irregular form, or else interspaces would be left, which is not found to be the case. Thus the "decussation of the prisms" seemed a plausible explanation of this appearance of striation; indeed, isolated prisms do present an appearance of slight varicosities, repeated at regular intervals. That the striation of enamel prisms is due to this cause is confirmed by Mr. Febiger, an American expert in the resolution of diatoms, to whom enamel sections were submitted for his opinion by Dr. Xavier Sudduth. That the striation of voluntary muscle is due to these

(1) The striation of voluntary muscle has been alleged to be due to this same cause (Dr. Haycraft, "Proceedings of Royal Society," Feb. 1881).

varicosities has been strongly urged by Dr. Haycraft ("Proc. of Roy. Soc.," 1881), and this is confirmed by Prof. Ewald, of Strasburg ("Nature," Nov. 1892), who finds that by pressing muscular fibre upon a film of moist collodion that substance reproduces the striæ, and that by overstaining with silver nitrate, so that the fibres are rendered absolutely opaque, it may be shown by reflected light, the surface appearing made up of regularly recurring hills and valleys. Von Ebner, however, holds that the cross striæ are due to the action of weak acid, and that the reason that they are seen in dry sections is that the Canada balsam in which they are usually mounted has a feeble acid reaction, and says that

FIG. 4 (¹).

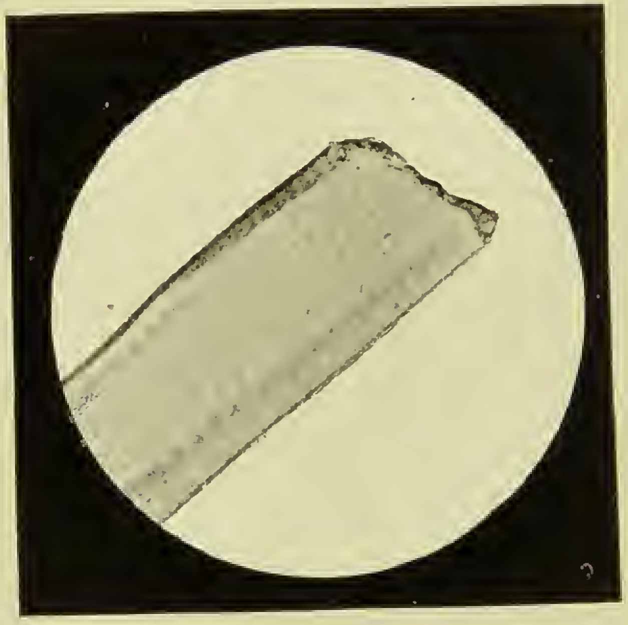


(¹) Striation of human enamel (from a photograph given to me by Mr. Leon Williams). The specimen was ground fresh, mounted in balsam, and not treated with acid at all.

a similar etched pattern may be produced by acids on some crystals.

He does not, however, infer that the prisms are therefore necessarily crystalline, but only that there are physical differences in their different parts; but this is controverted by Mr. Leon Williams and others, who have found the striation without acids or balsam being used.

Fig. 5 (¹).



Transverse striation is also to be seen on the prisms of the mollusc Pinna, which, from their large size and the ease with which they can be isolated, enable us to see that in their case it is apparently due to varicosities.

The analogy with the shell of Pinna must not be strained too far. Nevertheless, the resemblance of this prismatic structure to an enamel with prisms on a bigger scale, is sufficiently close to be in some measure instructive, although the prisms are composed of carbonate and not of phosphate

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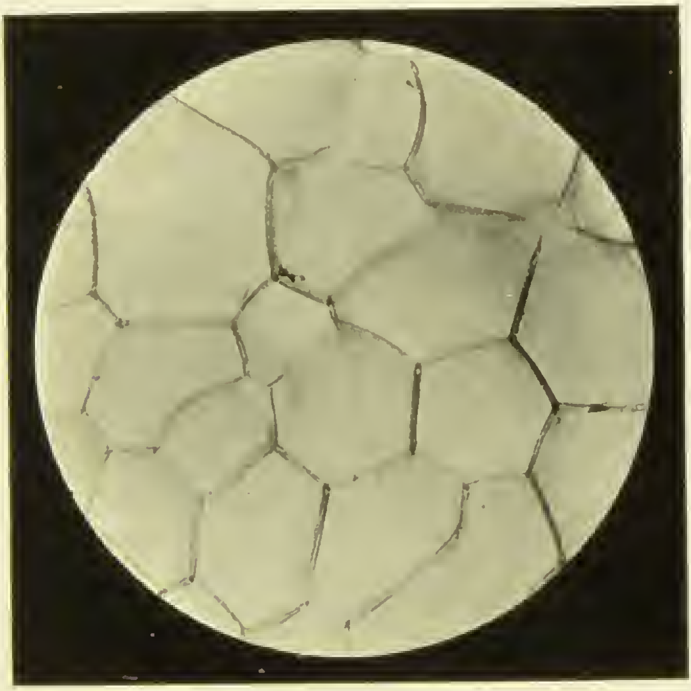
(¹) Isolated prism from the shell of pinna, showing transverse striation (photographed by Mr. Mummers).

of lime, and though nothing is known of their development. A transverse section of pinna shell shows the pattern produced by the approximation of the sharply defined prisms, but it is not possible to make out the existence of any interprismatic substance.

But if a section be rubbed down and cemented to the slide and then subsequently decalcified *in situ*, the prisms wholly disappear, the pattern being, however, still maintained by the organic honeycomb in which they lay, and by which, presumably, their form was moulded. If a piece of human enamel be similarly treated, nothing is left upon the slide, so that it is certain that whatever may have been the case during its formation, when it is finished the organic mould is gone. And here again the analogy fails in many respects, for it is probable that the organic

Fig. 6 (1).



(1) Decalcified matrix of pinna shell.

mould is of a quite different nature; indeed, as will presently be seen, little or no really distinct interstitial substance exists in the most complete enamels.

The recent researches of Mr. Leon Williams have thrown much light upon the structure of enamel, and illustrated as they are by very beautiful and untouched photographs, must be accepted as at all events indisputable as respects that which can be seen, although exception might be taken to his statement that photography can show all that the human eye can see. In a sense this is true, though, as Prof. Schäfer has somewhere said, it is with one's finger on the fine adjustment that, after all, the intimate structure of any tissue must be unravelled. Still, photographs have the unquestionable value that, unlike a drawing, they cannot be strained to express the preconceived ideas of the observer; on the other hand, high-power photographs represent truly only one plane, and appearances due to other planes out of focus in the thickness of the section occur, which may mislead, to say nothing of diffraction errors. His photographs completely demonstrate that enamel is a solid tissue, that is to say, that the minute canals said by von Ebner to exist in it have no real existence, and that this observer is also mistaken in supposing that the striation is an artificial appearance induced by re-agents.

Mr. Leon Williams believes that the completed enamel prism is a regularly beaded calcified rod, the beadings of which are the cause of the appearance of striation, and that these beaded rods are imbedded in a matrix which fills up all the interstices, is itself calcified, and does not differ much in refractive index from the prism itself. The varicosity of the rods and their consequent transverse striation is of variable distinctness; it is least seen, according to Mr. Leon Williams, nearest to the dentine.

The difficulty of deciphering the intimate structure of a transparent calcified material is very considerable at best, and, to borrow an illustration from Mr. Leon Williams, in enamel it is much as though we had made a complex pattern with beaded glass rods, then embedded them in melted glass of a lower melting point, and then set to work to unravel the pattern of the original rods.

According to Mr. Williams, each prism is composed of more or less globular masses arranged at definite intervals and united in their lengths by smaller rods or bands. The prisms thus built up touch, or almost touch, those around them, and the interstices, sometimes smaller, sometimes larger, are filled in with the matrix material. The varicosities in the rod lie in its length, and may be more or less fused together; those of one prism correspond with those of the next, and lie side by side and do not interdigitate with them. On the subject of the ultimate constitution of enamel Mr. Leon Williams thus expresses himself, "The entire mass becomes so completely calcified that in normal mature enamel there is left no trace of organic matter. Only the original form remains duplicated in mineral substances like a fossil."

Such, then, are the most recent views as to the nature of enamel, and they are confirmed by the action of orseille, a stain which will colour bone and dentine matrix, but which fails to impart the smallest tinge to enamel.

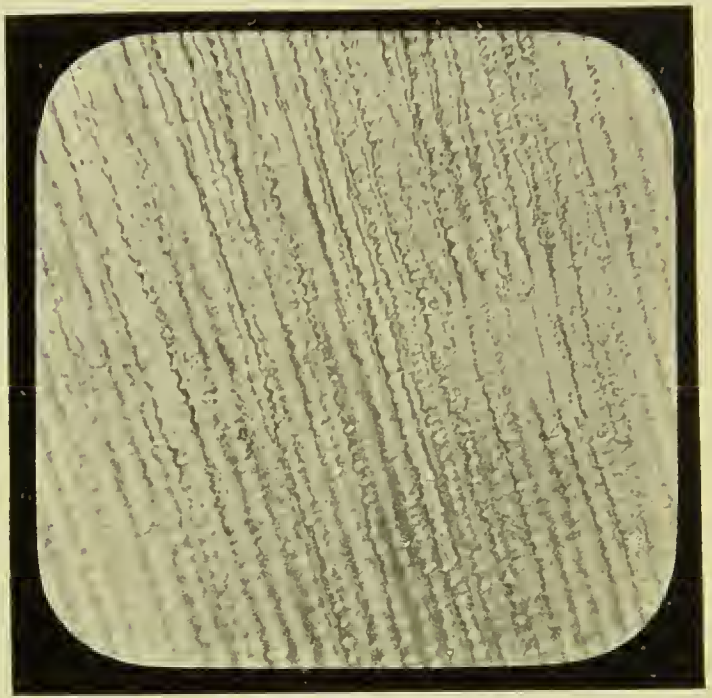
But although both alike appear to practically consist of salts alone, there seems to be a little difference between the prisms and the interprismatic substance which may be chemical or may be merely physical, for under the action of acids the prisms are at first rendered more distinct. Mr. Leon Williams believes that the acid acts first upon the interprismatic material, whilst other observers have thought the contrary; whichever be true, it is certain that the first effect is to render the prisms more distinct in appearance.

A curious appearance, rather inexplicable under the light of recent research, is sometimes, but not constantly, seen when enamel is subjected to the action of weak chromic acid ($\frac{1}{4}$ per cent.): the striation is rendered very plain, and the axes of the prisms are dark, and are stained green by the reduced chromium sesquioxide. In imperfect enamel, indeed, a central narrow canal is said to have been observed in the interior of an enamel fibre.

In fractured enamel, the line of fracture is said to run through the centre of the fibres, and not, as might have been expected, through their interspaces; but this I have not been able to verify.

There is also an appearance of striation upon a far larger scale, consisting of brownish lines, which are never, or very rarely, quite parallel with the outer surface of the enamel, but which nevertheless preserve some sort of relation with it and the surface of the dentine. These are known as the "brown striæ of Retzius," and, as they coincide with what was at one time the outer surface of the enamel cusp, are in some sense marks of its stratification in its original deposition.

Fig. 7 (1).



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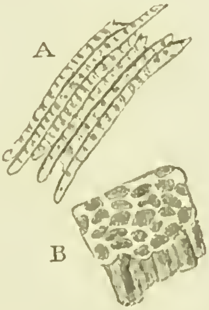
(1) Human enamel washed with dilute hydrochloric acid (photographed and prepared by Mr. Leon Williams). The beaded appearance of the enamel prisms is very clearly seen.

Von Ebner suggests that they are due to the entrance of air into spaces between rows of enamel prisms, but this is strongly controverted by Mr. Leon Williams, who not only denies the existence of spaces into which air could enter, but has pretty satisfactorily shown that they are not due to this cause but to a real pigmentation.

There is another class of markings seen upon the surface of a section of enamel, known as Schreger's lines; these are dependent upon the different directions of contiguous groups of prisms, and can only be seen by reflected light, and then only in longitudinal sections—by transmitted light they are quite invisible (von Ebner).

FIG. 8 (¹).



Cavities, or at least what look like cavities, of irregular form sometimes exist in the enamel near to the surface of the dentine, and when such spaces exist the dentinal tubes sometimes communicate with them; but these are perhaps to be regarded as pathological; Bödecker, of course, regards them as filled up by protoplasm. Irregular fissures and cavities also occur upon the outer surface of the enamel, which also have no special significance save as predisposing causes of dental caries.

In man, however, dentinal tubes may occasionally be seen to enter the enamel, passing across the boundary between the two tissues, and pursuing their course without being lost

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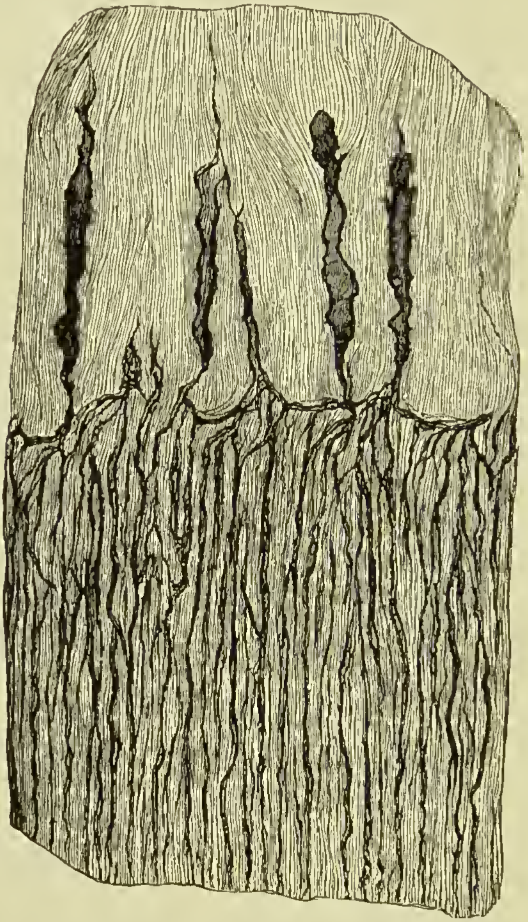
(¹) From human enamel, softened in chromic acid, until it could be readily cut with a knife.

in irregular cavities, though this appearance is seldom to be found. As was first pointed out by my father, the passage of the dentinal tubes into and through a great part of the thickness of the enamel takes place in marsupials with such constancy as to be almost a class characteristic.

Fig. 9 (1).



The only exception to the rule amongst recent marsupials occurs in the wombat, in which no dentinal tubes enter the enamel; those extinct marsupials which have been examined present, as might have been expected, a structure in this respect similar to that of their nearest allies amongst the recent genera.

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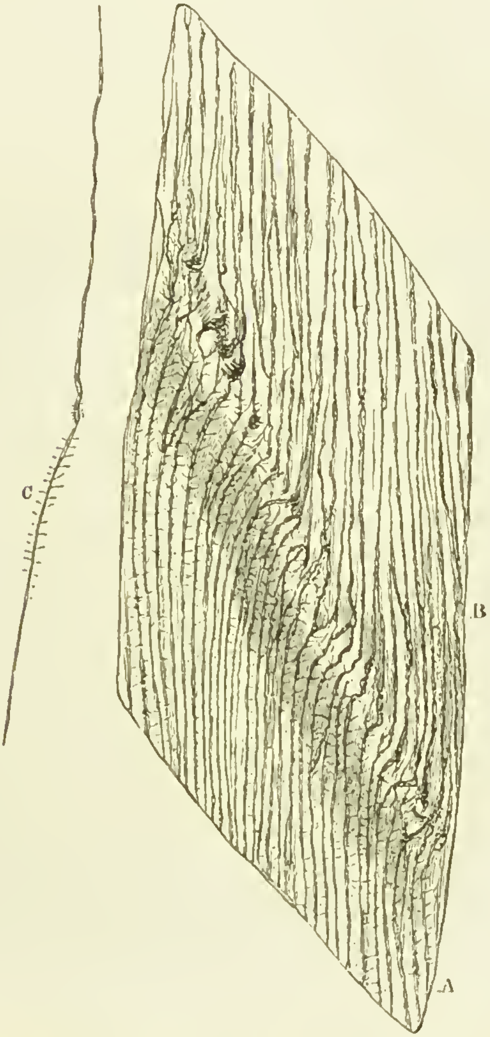
(1) Cavities in human enamel, which communicate with the dentinal tubes.

FIG. 10 (¹).



(¹) Enamel and dentine of a kangaroo (*Macropus major*).

The dentinal tubes in the dentine (A) are furnished with numerous short branches at the line of juncture with the enamel ; they are dilated, and a little bent out of their course, while beyond the dilation they pass on through about two-thirds of the thickness of the enamel in a straight course and without branches. Only a part of the whole thickness of the enamel is shown in the figure.

The enamel of the wombat is peculiar also in another respect, being covered by a strong and remarkably uniform layer of cementum.

The penetration of the enamel by dentinal tubes is not, however, a peculiarity quite confined to the marsupials, for it is to be found in some rodents (*e.g.* the jerboa), and in some insectivora (*e.g.* the *Soricidæ*), in Hyrax, and in a good many fish.

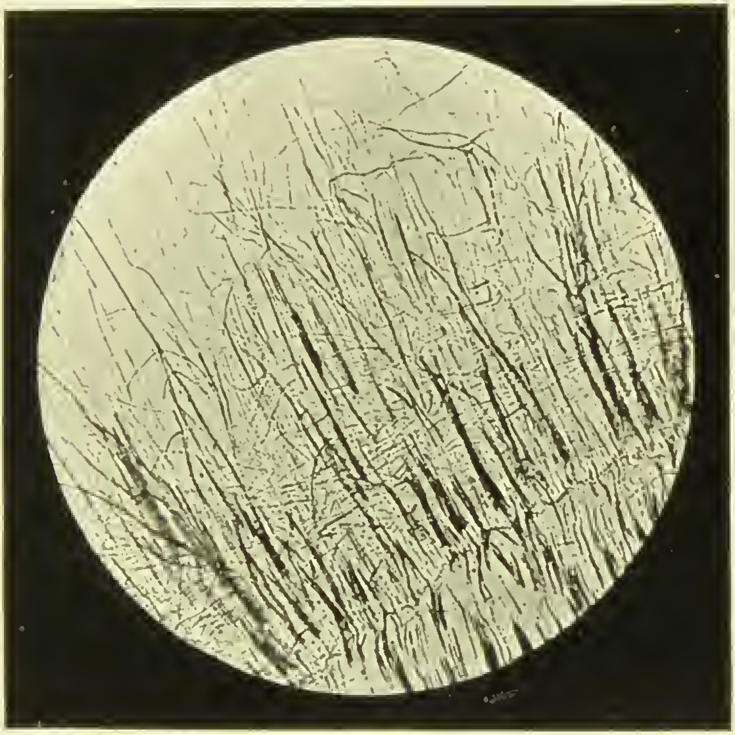
Waldeyer and Hertz doubt the passage of the tubes of the dentine into the enamel; as Kölliker observes, it is difficult to see how they can doubt it, even after mere observation of a single specimen; moreover, it is also capable of experimental demonstration, for if an acid capable of removing the enamel be applied to one of these sections of marsupial teeth so as to dissolve away the enamel, the freed tubes are left hanging out from the edge of the dentine, thus putting the matter beyond all possibility of doubt. The penetration of the enamel by tubes continuous with the dentinal tubes seems rather common in fish; these tubes in the enamel grow smaller as they leave the dentine and do not reach the exterior of the enamel; examples may be found in Serrasamo, in the barbel, and in many extinct fish.

The tubes run in the prisms and not between them, though it has been stated by von Ebner that the tubes in marsupial enamel do not lie in the prisms but in their interspaces, and he gives a figure of a transverse section in which all but one of the tubes appear to do so.

In relation to the development of enamel this question becomes important, but its solution is not quite so easy as might be supposed. For one thing, in proportion as the tube system is well developed, are the boundaries between the prisms indistinct; it is very difficult to get a thin transverse section of enamel, and when you have, it is difficult to see the tubes and the boundaries of the prisms. And the difficulty is immensely increased by the fact that the tubes are not straight, but are spirals, so that the least alteration of focus makes them wind about. But I have many transverse sections in which they appear to lie in the middle of the prisms, and by slight washing with acid the enamel section may be brought into a condition, in which both the interstitial substance and the tubes will stain with nigrosin, the latter much more strongly than the former. If such a longitudinal section be favourable, the interstitial substance looks granular and not very dark, nor very sharply bordered, while the tubes are very hard dark lines. They may then be seen to wind in and out of focus, but their longest lateral excursions only extend to the width of a prism and then they return again, so that I have satisfied myself that they are really in, and not between the prisms, a fact which tallies with my researches into the development of enamel to be described at a later page.

Although it has been usual to speak of marsupial enamel as penetrated by dentinal tubes, this is somewhat an improper use of terms. The enamel has a tube system, and its tubes are continuous with those of the dentine, but the tubes in the enamel are wholly and entirely an enamel formation,

Fig. 11 (¹).

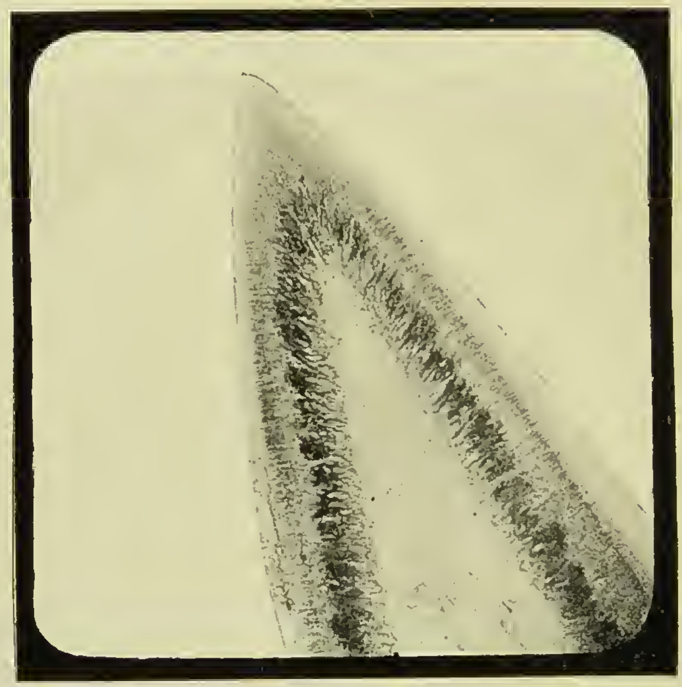


(¹) Enamel of Lepidotus, a fossil ganoid fish which existed from the Jurassic to the Tertiary periods; a small portion of dentine is seen at the bottom of the figure.

derived from the ameloblast cells, which at the first start of enamel development join up with the ends of the dentinal fibrils in the first-formed layer of dentine; or perhaps even earlier with the odontoblasts, before the formation of any dentine.

The penetration of enamel by tubes is met with in many fish, and some instructive examples may be met with in the sharks. In some fossil sharks, *e.g.* Spherodus, there is a rich crop of tubes in the enamel which are continuous with those of the dentine, and which become curiously curved as they course through the inner half of the enamel, but are lost before they reach its surface. And just about the time that I was myself leaning towards the same conclusion upon

Fig. 12 (1).



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(1) Tooth of Lamna. The outer layer, dark at its inner portion and transparent at the outer, consists entirely of enamel; the lighter central core is dentine.

FIG. 13 (¹).

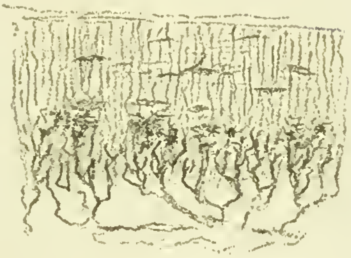
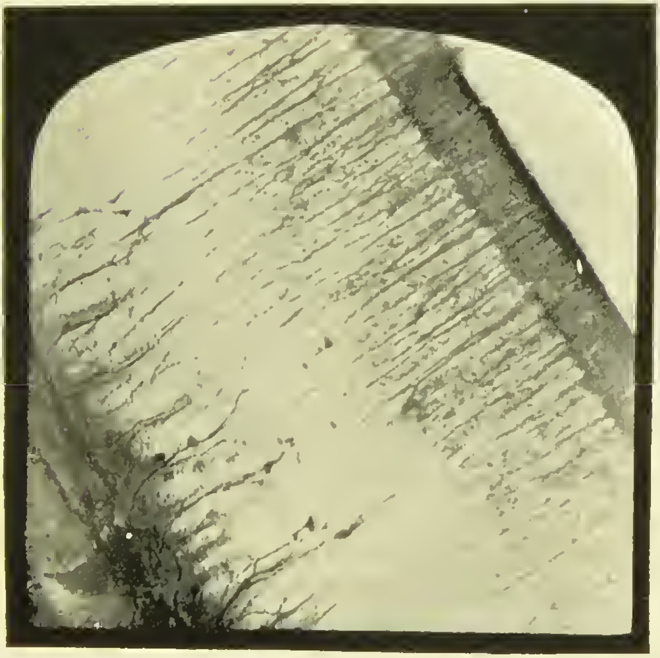


FIG. 14 (²).



other grounds, it was pointed out by Dr. Paul that I had probably been in error in describing the outer layer of the tooth of the Porbeagle shark (Lamna) as a layer of fine

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(¹) Enamel of Galeus (one of the Lamnidæ), showing penetration by tubes running in from the dentine.

(²) Enamel of a fossil shark (not identified) from the London clay. At the left hand bottom corner is a small amount of dentine; at the right upper side of the enamel is seen the distinct outer layer in which there is an appearance of tubes entering from the surface.

tubed dentine, and that it was probably enamel of the tubular variety.

Until the development of this layer has been fully worked out it is not possible to decide whether it be enamel or not, but as its physical and chemical characters resemble those of enamel rather than those of dentine, it has been placed amongst enamels in this work. But there are peculiarities in its development, which I am at present engaged in working out, which throw some doubt upon the propriety of including it amongst enamels as ordinarily understood.

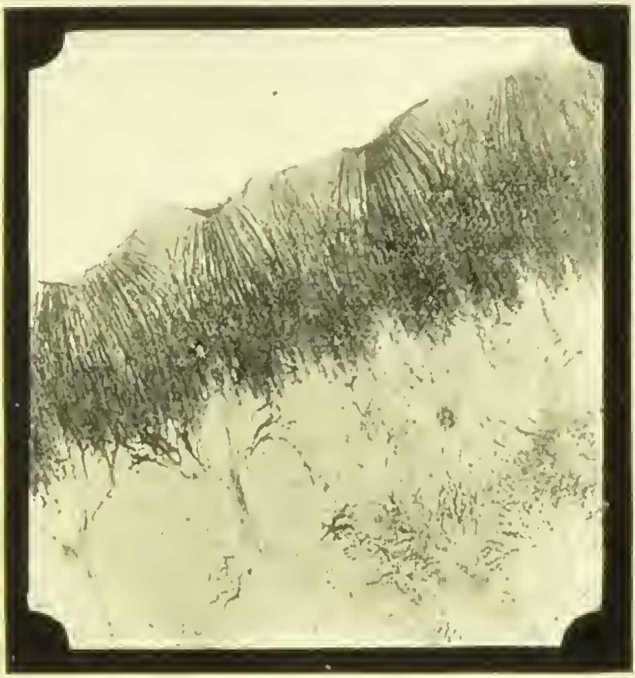
The surface of all dentine is apt to be somewhat festooned towards the enamel, and this is more so than usual; the dentine is of the osteodentine type, and so not very richly tubular, but some tubes do enter the enamel.

But besides these, the enamel has a rich tube system of its own, the tubes being much coarser than the dentine tubes, and about one third of the way through the enamel the tubes communicate with irregular lacunal spaces, a condition which I do not think has been noticed in enamel. These are both numerous and large, giving a confused appearance to this region; beyond it the tubes are continued on to the outer surface, near which there is a more or less differentiated layer. In *Galeus* this outer layer is much more distinct, and has every appearance of parallel tubes running in from the surface like those of Sargus (Fig. 16).

A fossil shark from the London clay, not identified, is yet more interesting. In this specimen the enamel is quite white, but the dentine has taken a strong brown stain, and shows clearly that the festooning of the dentine surface is carried further than in Lamna, so that tracts of dentine enter the enamel for some distance, their tubes going with them.

This at first sight would seem to lend probability to Dr. Paul's suggestion that the penetration of enamels by tubes from the dentine was to be explained by the dentine matrix growing in, and so carrying the tubes in between the enamel prisms. But, as I have shown elsewhere ("Phil. Trans.," B. 1897), this explanation cannot be universally true, seeing that the tubes in enamel are found developmentally to belong wholly to the enamel. The tubes are, some of them, traceable right through the enamel to its surface, but as they approach it they are in communication with a very small and very regular row of small spaces, and there is a very sharply defined outer layer. This and other fossil sharks show the same appearance of tubes entering from the surface; in fact they are larger at the surface than they are deeper in.

Fig. 15 (¹).



The archaic existing shark Cestracion has apparently this outer layer only. It has an enamel very peculiar, consisting of tubes running in from the surface, upon which they open with large mouths, and they are gathered into bundles, so as to make, as they radiate inwards, a well-defined pattern.

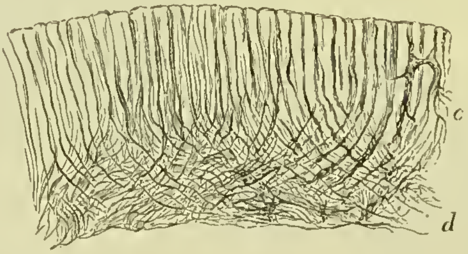
(¹) Enamel of Cestracion; the lower part of the figure consists of vascular dentine.

This tissue differs so strongly from the ordinary types of enamel that at first sight it might hardly be recognised as such, but comparison with the outer layer of the enamel shown in the preceding figure, and with that of Sargus, leaves no room for doubt as to its nature.

In the Sargus, or sheep's-head fish, for example, the enamel is penetrated by a system of markings which are not continued out of or derived from the dentine, but belong to the enamel itself.

These markings, as seen in the figure, run at right angles to the external surface of the enamel, proceed inwards without branch or bend for some little distance, and then, at about the same point, bend abruptly at an angle, and give off numerous branches. The meshwork produced by the crossing of the tubes at all sorts of angles in the inner part of the enamel is so complicated as to render it impracticable to reproduce it in a drawing. That portion of enamel next to the dentine is without any appearance of canals. Von Boas ("Zeits. f. wissen Zoolog.," Bd. xxxii.), describing similarly constructed enamel of scaroid fishes, says that I was in error in supposing that the canals open upon the outer surface of the enamel.

FIG. 16 (¹).



If a thin section be treated with dilute hydrochloric acid

(¹) Enamel and dentine of the sheep's-head fish (*Sargus ovis*).
The enamel is penetrated by a system of marks which enter from its free exposed surface, pass in for a certain distance in straight lines, and then abruptly bending at an angle cross one another, and produce a complicated pattern in the inner third of the enamel.

and watched during its action, short rods appear projecting from the surface, but they soon dissolve and disappear.

All these forms of tubular enamel, especially those in which the tubes open on and enter from the surface, were very unintelligible, as it was hard alike to see what advantage they could confer upon their possessors, or how they were developed. But if my conclusion as to the development of enamel (p. 160) be accepted, all difficulty of interpretation disappears. If all enamel in its development passes through a tubular stage, then these are merely arrests of complete development and perpetuations of a stage which is transitory in placental mammals.

CHAPTER II.

DENTINE.

The dentine makes up the greater part of every tooth which thus, even after the removal of the other tissues, would preserve somewhat its characteristic form. Several varieties of dentine exist in which those peculiarities of structure which differentiate it from bone are less marked, so that a point is sometimes reached at which it is hard to say whether a particular structure should more rightly be described as dentine or as bone. It will be most convenient to commence with the description of that variety of dentine which differs most markedly from bone, or, in other words, which has the most typical "dentinal" structure; and for that purpose the tissue met with in the teeth of man and the majority of mammalia (though it is by no means confined to that class), and known under the name "hard" or "unvascular" dentine, may be selected.

Dentine is a hard, highly elastic substance, in colour white, with a slight tinge of yellow; it is to some extent translucent, its transparency being often made more striking by contrast with the opacity which marks the first advent of dental caries. When broken a silky lustre is seen upon the fractured surfaces, which being in the main due to the presence of air in its tubes, is more apparent in dry than in fresh dentine; its fracture is sometimes described as finely fibrous.

The mass of the dentine consists of an organic matrix richly impregnated with calcareous salts; this matrix is everywhere permeated by parallel tubes, which radiate, with some minor exceptions, from the pulp cavity towards the surface of the tooth.

THE CHEMICAL COMPOSITION OF DENTINE.

The organic matrix or dentine, after the removal of the lime salts by an acid, is a yellow material of cartilaginous consistence, which when dried is not unlike horn; it is insoluble, and does not swell up in water, but when submitted to prolonged boiling dissolves, and is in fact converted into gelatine. It is similar to the substance obtained in like manner from bone, and consists of the substance known as collagen, a substance with a highly complex chemical constitution.

Collagen.—The white fibres of connective tissue, and the greater part of the organic matrix of bone, dentine and cementum, consist of this substance. Chemically it is nearly related to gelatine, of which it is the anhydride. By boiling in water for some little time it takes up an equivalent of water and becomes converted into gelatine; conversely, gelatine, by being heated to 130° C. (257° F.) may be dehydrated and converted into collagen.

$$\underset{\text{(Gelatine.)}}{C_{102}H_{151}N_{31}O_{29}} - H_2O = \underset{\text{(Collagen.)}}{C_{102}H_{149}N_{31}O_{28}}.$$

Elastin is another albuminoid substance which is abundant in ordinary elastic tissue. It is very insoluble, but may be dissolved by concentrated sulphuric acid, or concentrated nitric acid, or hot caustic potash, which, however, all decompose it. The linings of Haversian canals, of the lacunæ and canaliculi, and the sheaths of Neumann, are probably composed of this substance. It contains no sulphur, and thereby differs from keratin, which it in some respects resembles. Though insoluble in any fluid which does not decompose it, it is slowly digested by pepsin or by trypsin.

When the decalcified matrix of dentine is boiled so as to form gelatine a small insoluble residue is left, and the same result may be attained by treating dentine with an acid sufficiently strong to bring the collagen into solution; a similar result is obtained with bone.

This residue, which consists of a material singularly resistant to the action of acids and alkalies, appears to consist of elastin. In ivory, which is a highly elastic form of dentine, the elastin amounts to about 2·7 per cent. of the dried decalcified matrix, and it is, without doubt, as can be seen by a microscopic examination of the residue above alluded to, derived from the immediate walls of the dentinal canals or sheaths of Neumann, of which this residue wholly consists.

The collagen matrix is richly impregnated with lime salts, the great part of which are in the form of tribasic phosphate. In a fresh (wet) human tooth 62 per cent. of its weight was found to be inorganic salts, the tooth cartilage being 28 per cent., leaving a residue of 10 per cent. of water, which could be dried out at a temperature of 212° F.

Von Bibra gives the following analysis of perfectly dried dentine :—

Organic matter (tooth cartilage)	27·61
Fat	0·40
Calcium phosphate, and fluoride	66·72
Calcium carbonate	3·36
Magnesium phosphate	1·08
Other salts	0·83

Von Bibra gives another analysis :—

Cartilage	20·42
Fat	·58
Salts	1·00
Magnesium phosphate	2·49
Calcium phosphate, and fluoride	67·54
Calcium carbonate	7·97

And Berzelius gives—

Gelatine and water	28·00
Sodium salts	1·50
Magnesium phosphate	1·00
Calcium phosphate	62·00
Calcium fluoride	2·00
Calcium carbonate	5·50

Galippe gives—

Water and organic matter	25·29
Mineral matter	74·71
Soluble ash (alkaline chlorides, and phosphates)	·054

Calcium carbonate	0·35
Magnesium carbonate	1·13
Calcium	45·11
Magnesium	1·67
Phosphoric acid	23·7
Silicates	0·04
Undetermined	1·8

The dentine of many mammals is very much more rich in magnesium phosphate than human dentine is; even the latter, it would seem, from the discrepancies existing between the various analyses, is variable in composition, but, on the whole, it may be said that, amongst inorganic constituents of dentine, calcium phosphate largely preponderates; from 3½ to 8 per cent. consists of calcium carbonate; a much smaller proportion consists of magnesium phosphate, while calcium fluoride exists in traces only.

Great discrepancies exist in the amount of carbonates estimated, and this arises from the great practical difficulty in making a quantitative analysis of small proportions of carbonic acid in a substance of which only very small quantities are obtainable, sources of error, which cannot be eliminated, thus creeping in.

It is the opinion of Hoppe Seyler that the salt which chiefly hardens bone and dentine and enamel is a double salt, a compound of three equivalents of calcium phosphate with one of calcium carbonate, having an analogy with the mineral apatite.

Bone salt, $Ca_9\,(PO_4)_6$, $Ca\,CO_3$ or $Ca_{10}CO_3\,(PO_4)_6$.
Apatite, $Ca_{10}\,Fl_2\,(PO_4)_6$.
A variety of apatite, $Ca_{10}\,Cl_2\,(PO_4)_6$.

For a discussion of the probabilities of this being the case the reader is referred to Haliburton's "Physiological Chemistry," p. 494, and to papers by the author in "Journal of Physiology," 1896, and "Trans. Odontol. Soc.," 1896. The researches of Dr. Black ("Dental Cosmos," 1895), and of Dr. Galippe ("Soc. d. Biologie," 1884), indicate that the differences in the percentages of lime salts in various human teeth have been overestimated, and that there is but a very small range between the most perfect and the most frail teeth.

Ivory from the elephant tusk presents a low proportion of salts, not more than about 57·5 per cent., whilst the dentine of its molar contains about 70 per cent.

There is, however, an important source of error, which I have pointed out in the papers above referred to, in the estimation of the amount of the organic matrix. The usual method of estimating the salts is by ignition, that is to say, after fully drying the tissue at 212° F., burning away the organic matter, weighing the residual ash which contains all the salts, and setting down the loss as organic matter. In this way from 69 to 72 per cent. of salts is generally found, and dentine is usually said to contain from 31 to 28 per cent. of organic matrix.

But if, instead of doing this, we dissolve out the lime salts and then dry and weigh the collagen, we shall find that it falls far short of this, only amounting to about 19 per cent. of the dried dentine. The cause of this discrepancy, which has been long overlooked, is that dried dentine still contains something like 8 per cent. of water, which was held in chemical combination with the lime salt, and can only be driven out at red heat; in fact, the calcium phosphate, like any calcium phosphate prepared by wet methods, holds in combination one or more equivalents of water.

Thus fresh or wet dentine loses on drying at 212° F. about 10 or 11 per cent. of free water; then when ignited at bright red heat, it loses by decomposition of the hydrated salts 8 per cent. more, and to truly set down the composition of dentine we should write it—

Free water (which can be dried out at 212° F.)	10·0
Dry dentine	90·0
	100·0

And of dried dentine—

Organic matter	19·6
Combined water	8·4
Salts	72·0
	100·0

The proportion of salts to organic matter varies widely in different dentines; thus elephant ivory consists of—

Organic matter	34·0
Combined water	8·5
Salts	57·5
	100·0

Whilst the dentine of an elephant's molar contains a proportion of salts nearer to that of man—

Organic matter	21·0
Combined water	9·0
Salts	70·0
	100·0

In the matrix of human dentine there is, under ordinary circumstances, little, if any, structure to be made out; but the investigations of Mr. Mummery have shown that in caries of the teeth, which are then to some extent decalcified, an appearance like connective tissue fibres can be often seen in the matrix, and indications of the same thing can also be detected in some healthy dentine.

This observation, which accords with the descriptions by von Ebner of a similar connective tissue in the matrix of bone and of dentine, is strongly confirmed by what is seen in some Vaso-dentine. In this tissue the absence of a fine tube system renders it much more easy to see the nature of the matrix, which, under the influence of weak decalcifying agents, sometimes splits up into parallel fibres corresponding exactly in size and direction to the bundles of connective tissue fibrils which occur with complete regularity on the surface of the pulp.

Of the matrix of hard tubular dentine, then, we may say that there is normally no visible structure, but that it sometimes breaks up in such a manner as to indicate that there really is some trace left of connective tissue fibres which were once present.

The action of acids in decalcification tends to soften and make the connective tissues generally swell up and become less visible, hence the difficulty in establishing their presence.

The Dentinal Tubes.—As has been already mentioned, the matrix is everywhere permeated by tubes, the precise direction of which varies in different parts of the tooth, so that the following description of their course must be taken as merely in a general way descriptive, and not as of universal or precise application. Each tube starts by an open circular mouth upon the surface of the pulp cavity; thence it runs outwards, in a direction generally perpendicular to the surface, towards the periphery of the dentine, which, however, it does not reach, as it becomes smaller, and breaks up into branches at a little distance beneath the surface of the dentine.

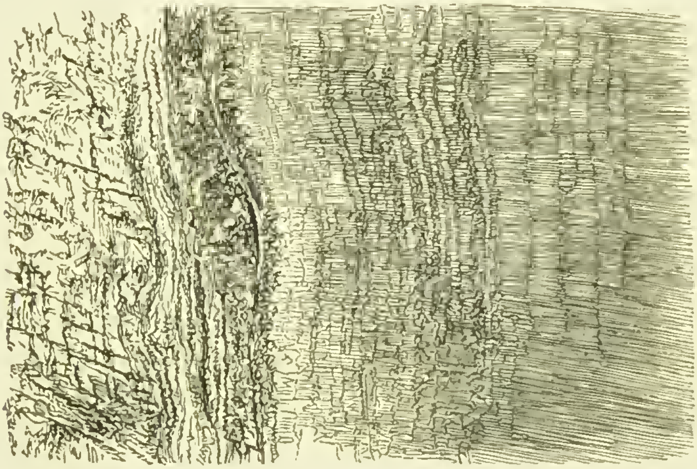
Near to the pulp they are so closely packed that there is little room between them for the matrix, while near to the outside of the tooth they are more widely separated: their diameter is also greater near to the pulp cavity.

The dentinal tubes do not pursue a perfectly straight course, but describe curves both on a larger and a smaller scale. The longer curves are less abrupt than the others, and are termed the "primary curvatures;" they are often compared to the letter *ƒ*, to which they bear a certain amount of resemblance; the primary curves are more pronounced in the crown than in the root.

The secondary curvatures are very much more numerous and are smaller; the actual course of the dentinal tube is, in most places at all events, an elongated spiral, as may be very well seen in thick sections transverse to the tubes; by alterations in the focus of the microscope the appearance of the tube making a spiral turn is made very striking. The effect of an elongated spiral viewed on its side will of course be only slight undulations, such as are the secondary curvatures of the tubes. The spiral course of the dentinal tubes is most strongly marked in the roots of teeth.

When a transverse section of dentine is viewed, bands or rings, concentric with the pulp cavity, are seen, and the same bands may be seen in longitudinal section. Such a striated or laminated appearance in the dentine may be due to two causes; and some little confusion has arisen in the nomenclature, owing to its double origin not having always been kept in view. Such striæ may be due either to the presence of rows of interglobular spaces, or to the coincidence of the primary curvatures of neighbouring dentinal tubes: that is to say, each tube bends at the same distance from the surface, and the bend makes a difference in the optical properties of the dentine at that point.

FIG. 17 (1).



Schreger described these latter: the lines of Schreger, therefore, are markings, ranged parallel with the exterior of the dentine, which are due to the curvatures of the dentinal tubes.

The "contour lines" of Owen, even in his own works, include markings of both classes: *i.e.*, those due to the curvature of the dentinal tubes, and those due to laminæ of interglobular spaces, such as are met with in the teeth of Cetacea. Retzius had seen and described contour markings due to interglobular spaces, though his name is not usually associated with them, the "brown striæ of Retzius" being markings in the enamel.

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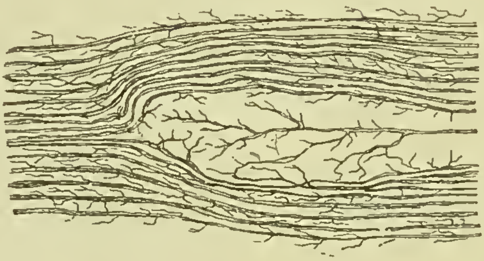
(1) Dentine and cementum of the narwal, showing contour lines due to rows of interglobular spaces.

The tubes as they pass outwards often divide into two equally large branches; they also give off fine branches, which anastomose with those of neighbouring tubes. In the crown of a human tooth these fine branches are comparatively few, until the tube has reached nearly to the enamel, but in the root they are so numerous as to afford a ready means of distinguishing whence the section has been taken. The small branches above alluded to are given off at right angles to the course of the main tube, which, however, itself frequently divides and subdivides, its divisions pursuing a nearly parallel course.

Fig. 18 (¹).



The tubes are subject to slight varicosities, and their course is sometimes apparently interrupted by a small interglobular space, as is to be seen in an extreme degree in the dentine of Cetacea.

Owing to their breaking up into minute branches, some of the tubes become lost as they approach the surface of the dentine, and apparently end in fine pointed extremities.

Some terminate by anastomosing with terminal branches of others, forming loops near to the surface of the dentine; others terminate far beneath the surface in a similar way.

(¹) Termination of a dentinal tube in the midst of the dentine—human.

Some tubes pass into the small interglobular spaces which constitute the "granular layer" described by my father, while others again pass out altogether beyond the boundary of the dentine and anastomose with the canaliculi of the lacunæ in the cementum.

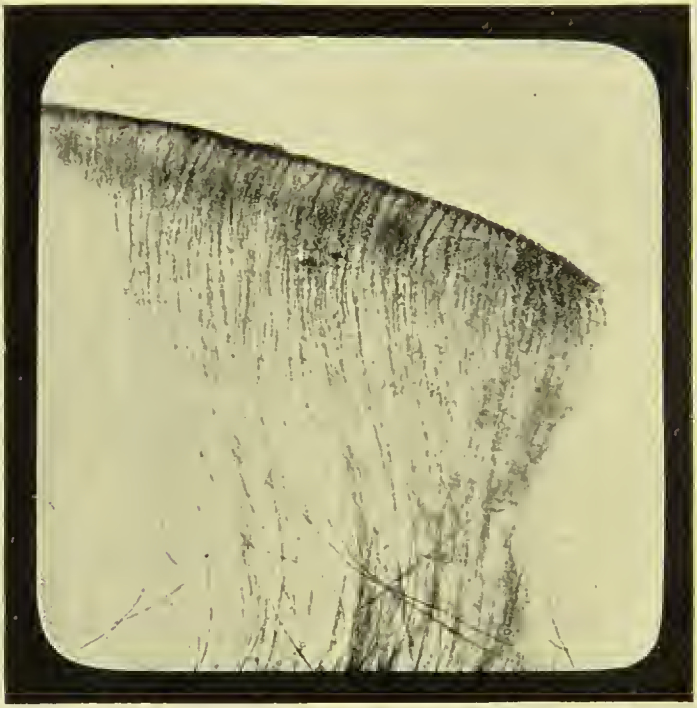
The enamel also may be penetrated by the dentinal tubes, though this, when occurring in the human subject, must be regarded as exceptional and almost pathological in its nature. (See Fig. 9.) As has, however, been mentioned in speaking of the enamel, in most of the Marsupials, in a good many fish, *e.g.*, Spherodus, Serrasalmo, Barbel, and in certain other animals it is a perfectly normal and indeed characteristic occurrence, difficult though it be to see how such a relation of parts is brought about in the course of development of the two tissues.

Dentinal Sheaths.—If dentine be exposed to the action of strong acid for some days, a sort of fibrous felt, or if the action of the acid has gone further, a transparent slime alone remains. Examined with the microscope, this proves to be a collection of tubes; it seems to be, in fact, made up of the immediate walls of the dentinal tubes, the intervening matrix having been wholly destroyed.

Two facts are thus demonstrated: the one that the tubes have definite walls, and are not simple channels in the matrix; the other, that these walls are composed of something singularly indestructible. Indeed, the walls of the dentinal tubes are so indestructible that they may be demonstrated in fossil teeth, in teeth boiled in caustic alkalis, or in teeth which have been allowed to putrefy.

Although Kölliker was, I believe, the first to describe and figure these isolated tubes, they are generally known as the "dentinal sheaths of Neumann," the latter writer having more fully investigated and described them. The precise chemical nature of these sheaths will be more conveniently considered under the head of calcification: similarly indestructible tissues are, however, to be met with surrounding the Haversian canals and the lacunæ of bone. It is the opinion of Neumann, as it was also of Henle, that the dentinal sheaths are calcified; but the proof of this is very difficult, as they cannot be demonstrated, or I should rather say, isolated, to any extent in dentine, unless it has been decalcified. Their existence as distinct from the fibrils has been recently denied by Magitot and by Dr. Sudduth.

FIG. 19 (1).

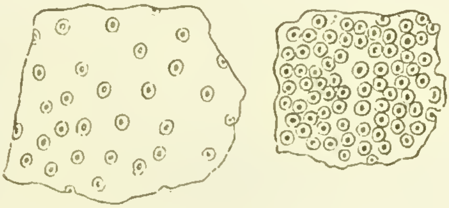


Transverse sections of dentine present fallacious appearances, owing to the thickness of the section giving to the tube a double contour which may be easily mistaken for a special wall. Immediately round the opening of the canal, or "lumen," as it is called, there is, however, generally a thin yellowish border, which may perhaps be the sheath of Neumann. In the earlier stages of caries, before the dentine is much softened, the walls of the canals become strikingly

(1) Ground section of human dentine, which has been submitted to the action of acids so as to isolate Neumann sheaths.

apparent. But it must be remembered that the dentinal sheaths can only be fully demonstrated by processes which amount to a partial destruction of the dentine, and that they are therefore, in some degree at all events, artificial; it may be that they have no real existence until they are brought into existence by the action of these agents. In that case all that we are entitled to say is, that the immediate surroundings of the soft fibril differ somewhat in chemical constitution from the parts of the matrix which are more remote, so that under the action of destructive agents the matrix may be split up into the sheathing layers round the fibrils and the more soluble residuum of the matrix.

FIG. 20 (¹).



Röse has succeeded, by Golgi's rapid method of nitrate of silver staining, in rendering Neumann's sheaths perfectly black, a transverse section of dentine thus prepared reminding one of the familiar tobacco-pipe appearance of dental caries, only that the sections of tobacco-pipe are black. As the intervening matrix remains unstained, it is clear that Neumann's sheaths differ from it in the degree of calcification, an interpretation which is borne out by the fact that in a longitudinal section the youngest dentine layer so stained is also intensely black.

If, prior to treatment by Golgi's stain, the tooth be prepared by Koch's (Weil's) method, the soft parts, including the dentinal fibres, do not take the stain, so that in the transverse section the fibril is seen as a bright point in the

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(¹) Transverse section of dentine. The appearance of a double contour is so much exaggerated as to make the figure diagrammatic, but it fairly represents the contour shown by nigrosin staining.

middle of the black Neumann's sheath. In longitudinal section the black sheath is fringed all along the course of the tubes by processes more or less bridging across to the next ones, but the dentinal fibrils have not been demonstrated in these branches.

Röse concurs in describing Neumann's sheaths as especially resistant to acids and also to caries; hence the distinctness of the "tobacco-pipe appearance."

And I myself have succeeded in satisfactorily staining them by means of nigrosin; a preparation so treated would resemble Fig. 20, save that the opening of the tube would be light, and be surrounded by an intensely black border in place of the light one of the figure.

Dentine would thus be considered as a tissue made up of a calcified matrix, analogous to that of bone, permeated by the soft fibrils, just as bone is permeated by canaliculi with soft contents, but having this peculiarity, that the latest formed portions of matrix, namely, those immediately embracing the fibrils, differ sufficiently from the bulk of the matrix in chemical constitution to enable them to be isolated as sheathing tubes, or to be stained *in situ*.

Dentinal Fibrils.—The canals which everywhere permeate the dentine are not empty, a fact which might be inferred from the difference in translucency and general aspect of dry and fresh dentine, whether seen in mass or in thin section; neither are they, as was at one time supposed, tenanted merely by fluid.

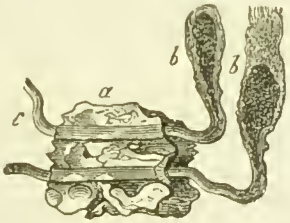
Each canal is occupied by a soft fibril, which is continuous with a cell upon the surface of the pulp; the existence of these soft fibrils was first demonstrated by my father, who thus, to use the words of Waldeyer, "opened the way to a correct interpretation of the nature of the dentine."

Henle, in his "Allgemeine Anatomie" (1841), a translation of a portion of which is to be found in the "Archives of Dentistry" (1865), figured and described projections from dentinal tubes. These he described as calcified and rigid, adding that by the use of acids they may be made flexible; he speaks of the tube as empty, save when blocked by granular calcareous matter, and alludes to fluids entering it by capillarity; and lastly, he says nothing whatever of the connections of the pulp with the tubes.

Müller (as translated in Nasmyth on the "Structure of the Teeth," 1839) says, "In breaking fine sections of the teeth perpendicularly to the fibres, I have frequently seen the latter projecting a little at the fractured edge. In such cases they are quite straight and not curved, and seem to be not at all flexible. Hence it follows that the tubes have an organised basis, a membrane, and that this is stiff and brittle, and probably saturated with calcareous salts, but weak and soft in a decalcified tooth."

The whole importance of my father's discovery lay in the fact that dentine is permeated by *soft, uncalcified structures;* and what is yet more significant, that these soft fibrils, permeating the hard dentine, proceed from the pulp. In no sense, therefore, did Henle anticipate this discovery.

Fig. 21 (1).



In 1854 Lent figured processes from the dentinal cells (odontoblasts) which he rightly conceived to be concerned in the formation of dentine; but in the earlier editions of the "Histology" of his friend and teacher, Prof. Kölliker, although Lent's discoveries are described and adopted without reservation, no mention of the real structure of dentine occurs. But in a later edition, Prof. Kölliker says, "After Tomes had described a soft fibre in each tube, I fell into the mistake of supposing that these fibres and the tubes were one and the same."

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(1) A fragment of dentine (*a*) through which runs the soft fibril (*c*), which issues from the odontoblast cell (*b*) (after Dr. Lionel Beale).

The circumstances under which the dentinal fibrils can or cannot be discovered are as follows, and may be taken as indications of a distinction between the dentinal fibrils and the dentinal sheaths.

If a tooth section be submitted to the action of a caustic alkali and boiled in it, or be allowed to completely putrefy, so that the soft parts are entirely destroyed, the dentinal sheaths can still be demonstrated, but the fibres can in no way be brought into view (Kölliker). The dentinal sheaths may be demonstrated also in fossil teeth, as has been shown by Hoppe ("Wurzburg Nat. Zeitschrift," Bd. VI. p. xi.) and others.

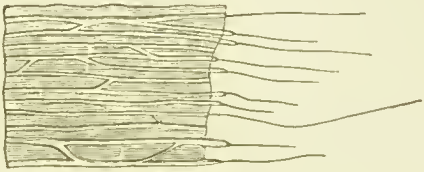
In fresh dentine every formative cell sends a process into the dentinal tubes (Tomes, Kölliker, Lent, Waldeyer, Neumann), and it has been found possible to demonstrate both the sheaths and the fibres in the same sections (Neumann, Boll).

In transverse and even in longitudinal sections of decalcified dentine the fibrils may be recognised *in situ* (Kölliker).

The contrast between the dentinal sheaths and the fibrils is this :—The sheaths are very indestructible, and can be demonstrated in teeth which have undergone all sorts of change ; the soft fibril is no longer demonstrable when the tooth has been placed in circumstances which would lead to its soft parts perishing. In dentine, then, we have (i.), a matrix permeated by canals ; (ii.) soft fibrils contained in these canals, or "dentinal fibres ;" and probably also (iii.) special walls to these canals or "dentinal sheaths ;" and it now remains to consider these in farther detail.

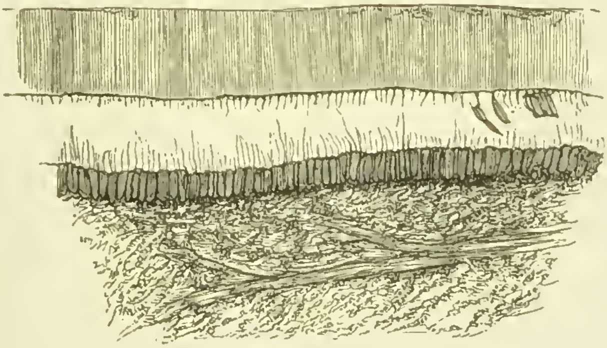
In fortunate sections of small fragments of dentine taken from the edges of the pulp cavity and including the surface of the pulp, the dentinal fibrils may be seen stretching from the cells of the superficial layer of the pulp (odontoblasts) into the dentinal tubes, as owing to these being extensile they may be stretched or drawn out from the tubes for some little distance without being broken across. In the same way they may be seen stretching across like harp-strings between two pieces of dentine, when this is torn by needles, and they can be thus shown in fresh fragments just as well as in those of decalcified dentine. When stretched to a considerable extent their diameter becomes diminished and they finally break, a sort of bead sometimes appearing at the broken end (J. Tomes). This would seem to indicate that the substance of the fibril is of colloid consistency, and that its external portions are in some degree firmer than its axial portion.

FIG. 22 (1).



The dentinal fibrils are well seen in the accompanying figure, in which some hang out from the edge of the dentine, whilst others have been pulled out from the dentine and are seen attached to the odontoblast cells.

FIG. 23 (2).



Modern methods of histological research have made the demonstration of the fibrils, which are continued from the odontoblast cells and enter the dentinal tubes, an easy matter; they are of some size, and, judging from appearances, are pretty firm in consistence, as they look somewhat stiff where they are seen projecting from the surface of a torn-away pulp.

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(1) Section of dentine from the edge of which hang out the dentinal sheaths, and beyond these again the fibrils (after Boll).

(2) Surface of the pulp, with the odontoblast layer *in situ*. The dentine fibrils pulled out of the dentinal tube hang like a fringe from the odontoblast layer : dentine fibrils are also seen hanging out from the edge of the dentine, to which, to the right of the figure, a few odontoblasts remain attached.

They do not stain very readily, although many stains are slightly taken by them; perhaps one of the best ways of staining them is to treat the tooth with a salt of iron followed by tannin, of course after a thorough washing.

The dentinal fibril is capable of being stained with carmine, though with some difficulty: in young dentine it is more easily stained, especially near the pulp cavity, and the accompanying drawing is taken from such a section of dentine from a half-formed human incisor. The matrix is slightly stained with the carmine, indicating that it has not yet become fully impregnated with salts, and in the centres of the clear areas dark spots deeply stained with carmine are to be seen, the latter being transverse sections of the dentinal fibrils *in situ.* I have observed precisely similar appearances in the thin young dentine of calves' and pigs' teeth; Kölliker also mentions that the dentinal fibril may be recognised *in situ* in transverse sections of fresh dentine.

Bödecker finds that the dentinal fibrils stain darkly with chloride of gold; when viewed in transverse sections under a magnifying power of 2,000 diameters they do not appear round but somewhat angular, and give off tiny lateral offshoots which seem to penetrate the dentine. In the matrix itself there is an appearance of a faint network when it has been stained with gold, and from this Bödecker infers that the dentine is penetrated everywhere by a network of living plasm, derived from, though far finer than, the dentinal fibrils. (Cf. results of Golgi's stain, p. 49.)

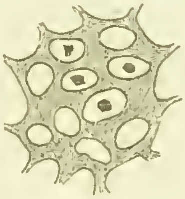
Probably the angularity of the fibril, which, as figured by him, is much smaller than the canal, is due to its having shrunk under the action of chromic acid or some such reagent.

According to Neumann, in old age the fibrils atrophy or become calcified; some observers have failed to detect them near to the periphery of the dentine, far away from the pulp cavity. But here they would naturally be more minute, and it is more probable that the manipulations had failed to demonstrate them than that they were absent; for Bödecker has traced them to the very outside of the dentine.

Dr. Beale has seen prolongations of the nucleus of the cell towards the base of the fibril, though in the example which he figures it does not enter it.

Dentinal fibrils were demonstrated in the Reptilia and Amphibia by Santi Sirena and myself; and by myself in the few fish that I have examined with that purpose.

FIG. 24 (1).



Of their real nature some doubts are entertained; they are certainly processes of the cells of the pulp, and their substance seems identical with that of the protoplasm of the cell, for they are of quite tolerably large size, and they are larger at their origin than further in. Nerves in the ordinary sense of the word they are not, and have never been supposed to be; but there are many examples of cellular structures which are connected with the termination of sensory nerve fibres, such as the goblet cells in the olfactory membrane of the frog, and it is quite possible that the odontoblast cells may stand in some such relation to the nerves of the pulp, the terminations of which have even yet never been satisfactorily traced.

Mr. Coleman once suggested that it was possible that the odontoblasts might have some tactile function, and Mr. Hopewell Smith ("Dental Record," August, 1889) points out their resemblance to multipolar ganglion cells of the spinal cord. According to Magitot the nerves of the pulp become continuous with a layer of reticulate cells which lie beneath the odontoblasts; and these freely communicate with the processes of the odontoblasts, so that there is a very direct chain of communication between the dentinal fibril and the nerves of the pulp. M. Magitot speaks very positively as to the accuracy of his views, which as yet, however, have not been confirmed by other investigators.

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(1) Transverse section of dentine; in four of the dentinal tubes, the dentinal fibrils, deeply stained with carmine, in the preparation from which this figure was drawn, are seen. The fibrils are somewhat shrunken, owing to the action of the glycerine in which the section is mounted.

Yet another view of the nature of the dentinal fibril is advocated by Klein ("Atlas of Histology," p. 183), who holds that the odontoblasts are concerned only in the formation of the dentine matrix, and that the dentinal fibrils are long processes of the deeper cells in the above figure, which run up between the odontoblasts and enter the dental canals. To this we shall have to recur in speaking of the pulp.

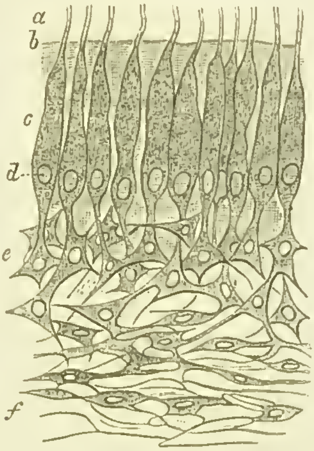
In a later paper ("Comptes Rendus," 1880) Magitot also impugns the accuracy of the views ordinarily accepted as to the structure of dentine, denying the existence of any special walls to the tubes, and further arguing that it is undesirable to think or speak of the channels in dried dentine as tubes at all. For, he argues, they are not tubes in the fresh state, seeing that the fibrils are adherent to the matrix and form a part of it, and that they were originally precisely the same tissue. He would prefer to speak of dentine as being a fibrillar tissue included in a hard and homogeneous matrix.

These views, however, do not differ substantially from those in the text, save that M. Magitot does not recognise the existence of that transitional tissue which others believe to be there, and call the sheaths of Neumann.

No true nerve fibril has yet been proved to enter the dentine; nothing but the dentinal fibril has ever been proved to pass from the pulp into the hard substance of the tooth; nevertheless, the observation of Boll is very suggestive. He found that by treating a perfectly fresh pulp with $\frac{1}{5}$ per cent. solution of chromic acid an immense number of fine fibres could be demonstrated, a great many of which projected from above the surface, as though they had been pulled out of the dentinal tubes, but although they pass up from a plexus of dark-bordered nerve fibres beneath the membrana eboris between the cells of that layer, their passage into the dentine remains a mere matter of inference.

Be that as it may, there can be no question that the sensitiveness of the dentine is due to the presence of soft organised tissue in the tubes, and is not a mere transmission of vibrations to the pulp through a fluid or other inert conductor. The peripheral sensitiveness of a tooth can be allayed by local applications which it would be absurd to suppose were themselves conducted to the pulp; moreover, it is within the experience of every operator that after the removal of a very sensitive layer of caries, you often come down upon dentine, which though nearer to the pulp, is far less sensitive, a condition quite inexplicable, except upon the supposition of a different local condition of the contents of the tubes. Irritation applied to the dentinal fibrils may be

FIG. 25 (1).



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(1) After Magitot. *a.* Dentinal fibrils. *b.* Amorphous matrix. *c.* Odontoblasts. *d.* Nuclei of odontoblasts. *e.* Stellate cells. *f.* Nerve extremities which are continuous with the branched cells.

propagated to the pulp, and irritation of the pulp set up without any real exposure of the latter.

With reference to the probabilities of actual nerve fibres entering the dentinal tubes, it must be remembered that, in those tissues which are naturally so thin as to present great facilities for examination, nerves of a degree of fineness unknown elsewhere have been demonstrated; in other words, the easier the tissue is to investigate, the finer the nerves which have been seen in it, while dentine is among the most difficult substances conceivable for the demonstration of fine nerve fibrils, if such exist in it.

And Mr. Mummery's iron preparations clearly show that fine fibres traceable into connection with indisputable nerve bundles deeper in the pulp do run out straight towards the dentine and right up to it as though they entered it. In this connection the very remarkable specimens of Dr. Dentz, of Utrecht, may be mentioned. These, which were cut from embryos while about half the thickness of the dentine was formed, show pear-shaped bodies arranged with regularity a short distance within the border of the dentine, the smaller end being directed towards the pulp, and being at their small ends connected with one or more dentinal tubes. These pear-shaped bodies have two or three large nuclei, and present a close resemblance to some forms of nerve-end organs.

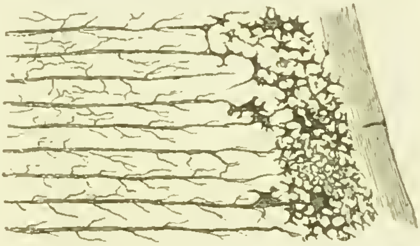
Amongst many difficulties as to their interpretation is the fact that the examination of a large number of sections of dry temporary teeth has quite failed to reveal the spaces which might have been expected to have contained them, and their relatively large size ($\frac{1}{400}$ of an inch) would render the spaces conspicuous. A fuller description of these bodies will be found in the "Transactions of the Odontological Society," 1892.

Interglobular Spaces.—In the layer of dentine which underlies the cement an immense number of these spaces exist, giving to the tissue as seen under a low power an appearance of granularity. On this account my father gave to this the name of the "granular layer" of dentine; on account of the far greater abundance of the spaces in that situation, it is far more marked beneath the cement than beneath the enamel, and many of the dentinal tubes end in these spaces.

Although the name "interglobular spaces" is strictly applicable to the structures constituting the granular layer of dentine, it was not to these that it was first applied. When a dried section of dentine is examined, dark irregular spaces clustered together and usually most abundant at a little distance below the surface, are often to be seen, particularly if the section has been made from a brownish, imperfectly developed tooth.

These spaces have a ragged outline, furnished with short pointed processes, and in favourably prepared sections it may be seen that their outlines are formed by portions of the surfaces of closely apposed spheres, and globular contours may often be detected in the solid dentine near to them, as is seen in Fig. 27, taken from a section boiled in wax in order to render it very transparent.

FIG. 26 (1).

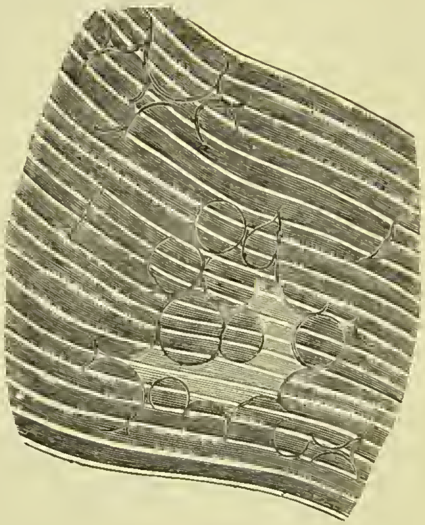


Although these large spaces are very common, they are perhaps not to be regarded as perfectly normal, but are rather indications of an arrested development at that spot. The occurrence of globular forms during the early stages of calcification, will again be alluded to in connection with the development of teeth; but although the term "interglobular" is thus strictly applicable, the use of the word "spaces" is not so correct. In dry dentine it is true that they are, as Czermak described them, spaces filled with

(1) Dentinal tubes terminating in the spaces of the granular layer.

air; but that they are so is only due to the fact that their contents are soft, and shrivel up in drying. In the fresh condition the interglobular "space" is perfectly full, its contents often having the structural arrangement of the rest of the matrix, or else consisting of soft plasm; in the former case, the dentinal tubes pass across and through it without any interruption or alteration in their course. This fact, as well as the softer nature of the contents as compared with the rest of the dentine, is well illustrated by a section in my possession which was taken from a carious tooth, near to the affected surface. In this the fungus had effected an entrance into some of the tubes, giving to them a varicose beaded appearance, and causing their enlargement. But when it reached the interglobular space, the less amount of resistance, or possibly the more favourable pabulum accessible, led to its more rapid development, so that the tubes within the confines of the space are many times more enlarged than those outside; nevertheless the continuity of the tubes across the space is well demonstrated by the growth of micro-organisms having followed them with exactitude.

Fig. 27 (¹).



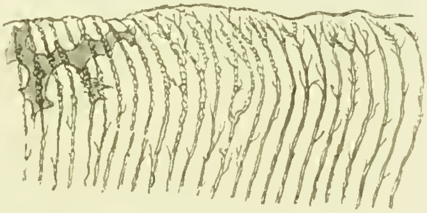
(¹) Interglobular spaces in dentine.

It sometimes happens that indications of spherical forms and faintly discernible contours resembling those of the interglobular spaces may be seen in dried sections, in which no actual spaces occur. The appearances are perhaps produced by the formation of an interglobular space, the contents of which have subsequently become more or less perfectly calcified: the term "areolar dentine" sometimes applied to this has fallen into disuse.

Globular forms, in concentric layers like an onion, are very distinct in the outer part of the dentine in some fossil reptiles. (Credner, "Abhandl. Math. Phys.," 1893, Leipzig.)

The exact nature of the contents of the interglobular spaces is not very certain: they may, with some difficulty, be tinted by carmine, and it is said that they may, like the dentinal sheaths, be isolated by the destruction of the rest of the matrix in acids. Like Neumann's sheaths, they take a deep black stain with Golgi's process.

Fig. 28 (¹).



Bödecker says that there is soft living plasm abundantly distributed in the smaller interglobular spaces which constitute the granular layer, and this is in very free communication with the soft fibrils in the tubes on the one side and with the soft contents of the lacunæ and canaliculi of the cementum on the other.

In the dentine so far described, which is that variety known as hard or unvascular dentine, some degree of nutrition is perhaps provided for by the penetration of the whole thickness of the tissue by protoplasmic fibres, the

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(¹) Section of carious dentine, in which some of the tubes are beaded by the ingress of organisms, which have developed with greater freedom in one or two of the tubes where they cross the interglobular spaces.

dentinal fibrils; but this nutrition may be effected in a different way, and there are other varieties of dentine known in which dentinal fibrils have never been shown to exist. For descriptive purposes I would classify dentines as

(i.) Hard or unvascular dentine.
(ii.) Plici-dentine.
(iii.) Vaso-dentine.
(iv.) Osteo-dentine.

Ordinary hard dentine has been sufficiently described; plici-dentine is a variety of it, not very distinct in its essential nature, though at first sight widely dissimilar.

Plici-dentine.—In ordinary dentine the dentinal tubes radiate out from a pulp and pulp chamber of simple form; render that form complex by foldings of its walls, the dentinal tubes still running off at right angles to that portion of pulp to which they immediately belong, and we have a "plici-dentine." It is merely an ordinary dentine with its pulp folded up and wrinkled into a greater or less degree of complexity.

In the teeth of the Varanus (monitor lizard), or in Lepidosteus, for example, the process of calcification of the pulp takes place in such manner that in the upper half of the tooth a cap of ordinary unvascular dentine, in which the tubes radiate from a single central pulp cavity, is formed. But in the lower part of the tooth slight longitudinal furrows appear on the surface, which, on transverse section, are seen to correspond to dippings in of the dentine; and the dentine is, as it were, in folds. The pulp on section might be compared to a paddle-wheel, the floats of which correspond to the thin flat radiating processes of pulp; but as yet the central pulp chamber is unaltered. In Lepidosteus, a little lower down, as represented in Fig. 31, there is no longer a central simple pulp chamber; the inflections round the periphery have become relatively much deeper, and the centre of the tooth is occupied by a tissue irregular, but not otherwise unlike the dentine of Myliobates; that is to say, there are a number of columns of pulp, each of which forms the axis whence a system of dental tubes radiate.

The outrunning plates of dental pulp, which on section radiate out like the spokes of a wheel, do not always remain single; they may divide simply into two branches, as may be seen in the section across the base of the tooth of Lepidosteus (North American bony pike); or sometimes there are several branches.

FIG. 29 (¹).

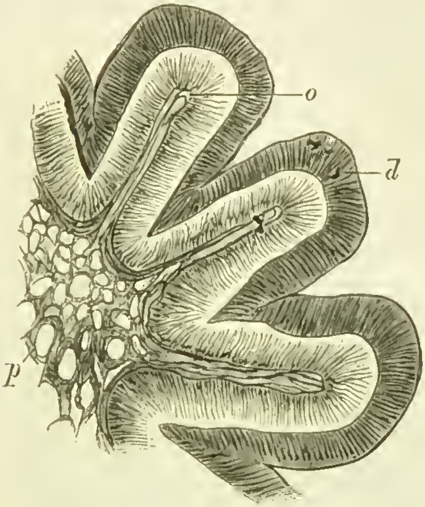
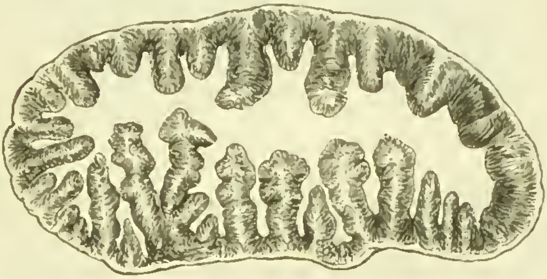


FIG. 30 (²).



In Lepidosteus oxyurus there are simple inflections, and

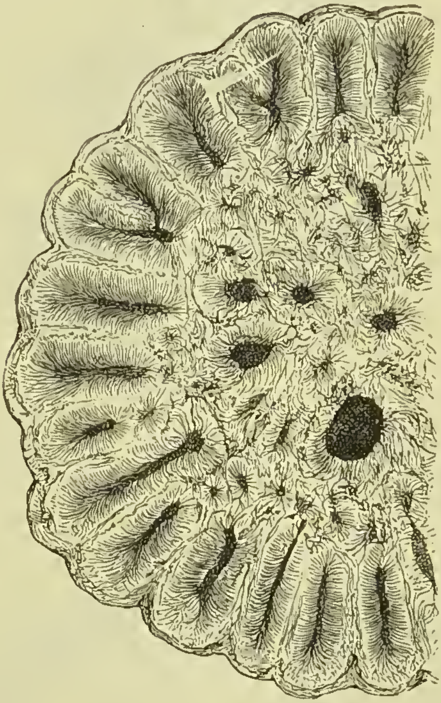
(¹) Section of plici-dentine with the pulp *in situ* (Lepidosteus). *o.* Odontoblasts. *p.* Connective tissue framework of pulp. *d.* Dentine.

(²) Transverse section across the crown of the tooth of Varanus, near to its base. The central pulp cavity is produced out into processes, and it might be said the dentine is arranged in plates with some little regularity round its periphery.

a central pulp cavity; in L. spatula the inflections are branched, and the central pulp cavity all filled up.

In the accompanying figure of the base of a tooth of Lepidosteus some few of the outrunning pulp chambers are seen to be bifurcated, while the central mass of the tooth is composed of dentine permeated by pulp canals which pursue a longitudinal course; a slight further modification brings us to the structure of the dentine of the Labyrinthodon, in which a maximum of complexity is attained, although a clue to its intimate structure is afforded by the teeth of Varanus or of Lepidosteus.

FIG. 31 (1).



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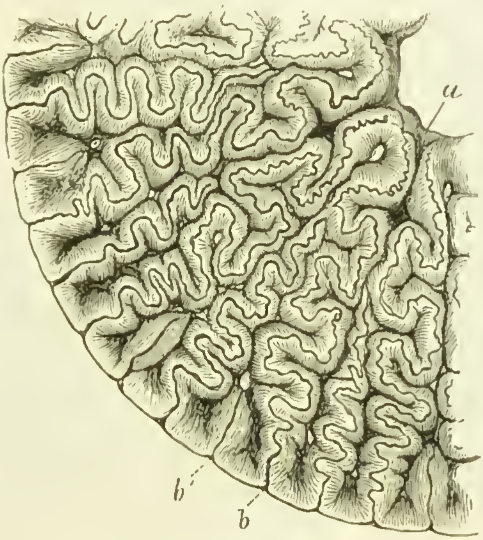
(1) Transverse section across the tooth of *Lepidosteus spatula.* At the exterior are regularly disposed radiating plates of dentine, each with its own pulp cavity, while the central area is composed of more or less cylindrical pulp chambers, each of which forms the starting point for its own system of dentinal tubes. The pulp chambers are made dark in the figure for the sake of greater distinctness.

The laminæ of pulp, with their several systems of dentinal tubes, instead of passing out in straight lines like the spokes of a wheel, pursue a tortuous course as they run from the central small pulp chamber towards the surface. Not only do they undulate, but they also give off lateral processes; and at their terminations near to the surface of the tooth, the thin laminæ of pulp (so thin that the radiating pulp chambers are mere fissures) become dilated; so that on section circular canals are seen at these points, as is also the case at the points where subsidiary processes branch off.

FIG. 32 (1).



The wavy course pursued by the radiating plates of dentine, and the disposition of the tubes round the dilated portions of pulp chamber, render the general aspect of the dentine structure very complicated; the several "systems" (2) are united to one another by an inosculation of the terminal branches of the tubes in some few places, but more generally by a clear layer containing radiate spaces, something like the lacunæ of cementum. Hence Professor Owen has described the tooth as consisting of radiating plates of dentine, between which pass in equally convoluted plates of cementum. But, as was pointed out by my father ("Phil. Trans.," 1850), the mere presence of lacuna-like spaces is not sufficient to prove the presence of cementum, inasmuch as they occur on a small scale in the granular layer of dentine; moreover, when cementum and enamel are both present, the cementum is always outside the enamel, whereas at the upper part of the tooth of the Labyrinthodon the characteristic inflections take place within a common investment of enamel which does not dip in. Thus the whole of the

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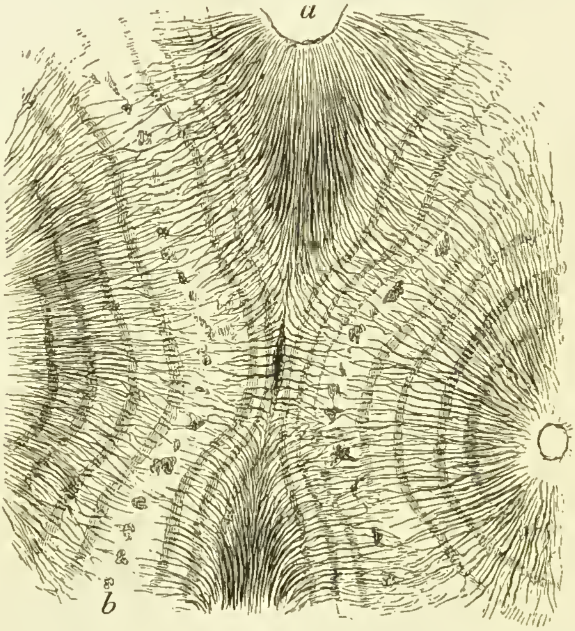
(1) Transverse section of a tooth of Labyrinthodon. (After Owen.) The letter *a* is placed in the centre pulp chamber; the letter *b* marks the lines of separation between the system of dentinal tubes which belong to each lamina of pulp; these lines of demarcation were formerly supposed to be occupied by cementum.

(2) The term "dentinal system" is applied to the portion of dentine in which all the tubes radiate from a single section of pulp chamber; thus the tooth of Labyrinthodon is made up of many dentinal systems; the same thing may be said of the tooth of Myliobates.

FIG. 33 (1).



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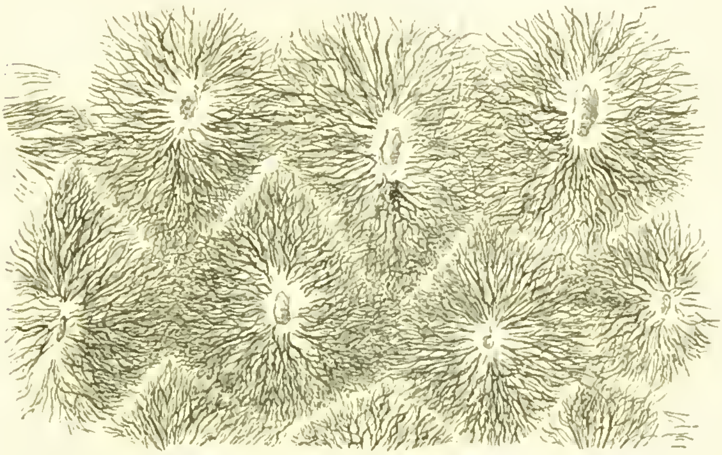
(1) From tooth of Labyrinthodon, showing the nature of the connection between the contiguous dentinal systems. (After a drawing of my father's.)

tissue constituting the very complex pattern of the Labyrinthodon tooth is dentine, and the cementum does not, as was usually supposed, enter into its composition at all.

Another form of dentine, in some respects akin to plicidentine, is exemplified in the teeth of Myliobates, a large ray; or in the teeth of the rostrum of the saw-fish (Pristis).

In the Myliobates (Fig. 34) the flat pavement-like tooth is permeated by a series of equidistant parallel straight canals, running up at right angles to the surface; from the upper end and sides of these channels systems of dentinal tubes radiate, just as the tubes radiate from the single pulp chamber of a human tooth, save that they run for a comparatively short distance. In tranverse sections the tubes are seen radiating from these channels, and at their terminations sometimes inosculating with the terminal branches of the tubes of another system. The channels contain prolongations of the vascular pulp, which are distinct in the upper part of the tooth, but intimately united together at its base, where the disposition of the channels ceases to be regular, and, as a consequence, the systems of dentinal tubes pass from them in various directions without producing

FIG. 34 (1).



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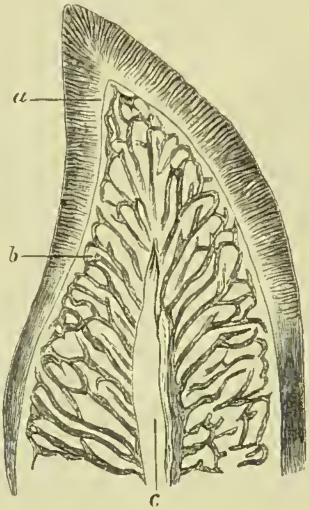
(1) Transverse section of the dentine of Myliobates.

the symmetrical patterns which characterise the upper part of the crown.

When the tooth comes into use and its immediate surface gets worn off, the ends of the perpendicular pulp channels would be laid open, were it not that they become blocked by the deposition of a transparent homogeneous tissue within them, analogous to the similar tissue which closes the Haversian canals of an antler about to be shed.

FIG. 35 (1).



Instead of being regarded as a plici-dentine, such a tooth might be said to be built up of a series of small parallel fused denticles; and a similar structure is presented by the rostral teeth of the saw-fish, and by the teeth of the Orycteropus or Cape ant-eater.

Vaso-dentine.—In dentine, as so far described, the existence of a system of fine tubes, dentinal tubes, has been the most conspicuous feature, but there are tissues equally entitled to be called dentine in which no such tube system exists at all.

But, as it would seem necessary that some living material should permeate any tissue which is for any length of time to be retained in close connection with the rest of the organism, these dentines are not solid, but are permeated by a much larger tube system, the canals being in this case channels through which capillaries course, and through which red blood circulates, so that during the life of the animal the teeth look quite pink, and in a section cut from the fresh tooth the coats of the capillary may be seen to hang out from the edge, and the canals to be full of blood corpuscles. The arrangement of the vascular canals is regular and striking, reminding one of the appearance of the vessels in an intestinal villus; in fact, an intestinal villus petrified, whilst its capillary network remained pervious, and red blood continued to circulate through it, would form no bad representation of a typical vaso-dentine tooth.

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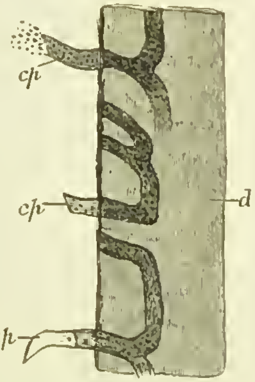
(1) Tooth of Ostracion. *a.* Enamel. *b.* Capillary channels. *c.* Axial pulp chamber.

Fig. 36 (1).



In all the vaso-dentine teeth with which I am acquainted, the pulp chamber is of simple form, so that the conical pulp can be pulled out, and no tissue, or next to none, save the blood-vessels, enters the canals, which are therefore of almost uniform diameter, and each capillary almost or quite fills and fits its canal.

The matrix does not present a very definite structure, though there is generally some appearance of lamination parallel with the surface, and what has just been said with reference to the canals requires modification in so far as

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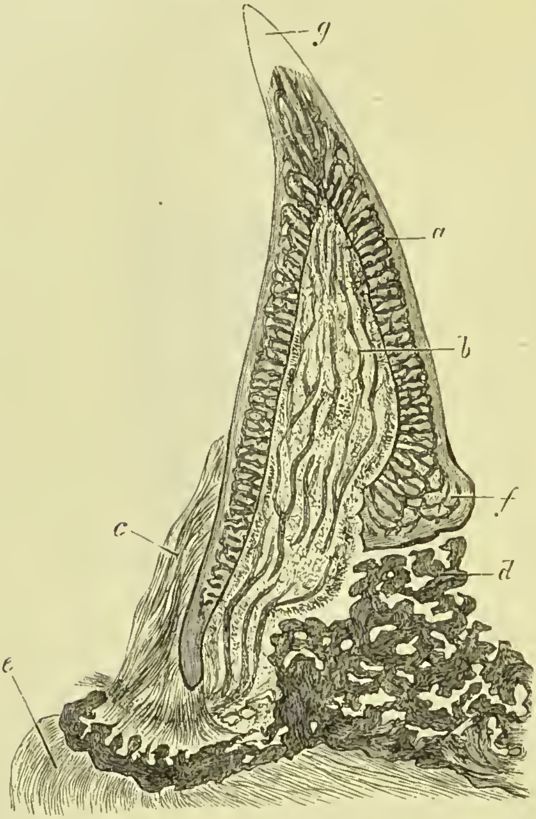
(1) Section of dentine from a freshly caught Hake. *d*. Dentine matrix. *cp*. Capillary channels with blood-vessels hanging out from the edge, containing here and there abundant blood corpuscles.

FIG. 37 (¹).



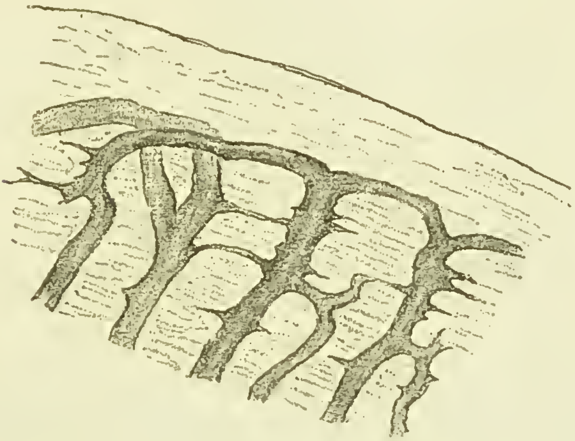
there are in dry specimens slight narrow spaces, thorn-like in section, which run from the canals in between the laminæ. (See Fig. 38.)

These are not present in all vaso-dentines, but may be found in a good many, as, for example, in the hake, from which the figure has been drawn.

(¹) Hinged tooth of hake. *a.* Vaso-dentine. *b.* Pulp. *c.* Elastic hinge. *d.* Buttress of bone to receive *f*, formed out of bone of attachment. *e.* Bone of jaw. *f.* Thickened and rounded free base of tooth. *g.* Enamel tip.

As a rule the vascular canals do not extend quite out to the surface, but terminate sometimes in a bounding canal, and sometimes without one, at a very definite distance within the surface; this perhaps represents the original limit of the capillaries in the formative pulp; but however that may be, the structure of the matrix outside them is, in some examples, very interesting in view of recent investigations into the development of dentine (see Fig. 39), for this outer layer looks exactly like a calcified connective tissue which has preserved all its form, and it is not obscured by the occurrence in it of any tube system, inter-globular spaces, or other structures.

Fig. 38 (¹).



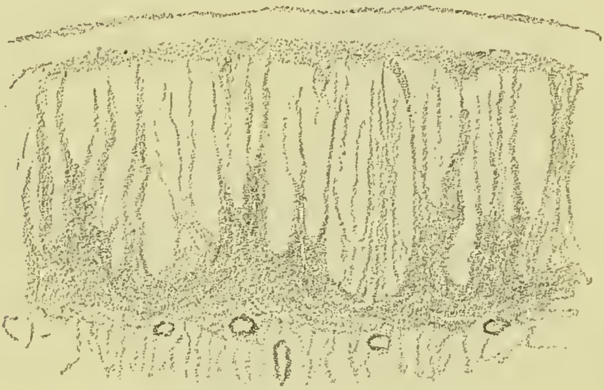
Such in brief are the characters of a typical vaso-dentine, but there are vast numbers of forms of this tissue which serve to bridge over the gap which would seem to exist between it and hard dentine. Thus in the conical teeth o the flounder, and indeed of many flat fish (*Pleuronectidœ*) we find the tips of the teeth to be composed of ordinary fine tubed dentine, surmounted by enamel tips. In this part of the tooth the tubes radiate outwards in the ordinary way from the pulp chamber, and are both numerous and regular,

(¹) From a tooth of the hake. The thorn-like processes are seen, as also a faint lamination of the matrix.

but lower down in the tooth the dentinal tubes become less numerous, and *pari passu* with their diminution, vascular canals begin to make their appearance till, as we reach the base of the tooth, we find tolerably typical tubeless vaso-dentine.

We may suppose, therefore, that the two sorts of tubes are capable of taking the place of one another, and that the nutrition of the dentine may be provided for either by protoplasmic material running for a long distance from the pulp through dentinal tubes, or by blood brought nearer to hand by the vessel-carrying canals, but that both are not required, and so do not co-exist in full development.

Fig. 39 (¹).



But from the flounder's tooth we may learn that hard dentine and vaso-dentine are not fundamentally dissimilar, and that they may run into one another by imperceptible gradations, so that we cannot say exactly at what point we are to give it the name of vaso-dentine. And within the limits of a single family of fish—the Gadidæ or cod-fish family—there are to be found all grades of vascularity, from the complete and regular system of vascular channels existing in the hake, to the sparse canals of the haddock and the pollack; in Lotella there are neither dentinal tubes nor vascular canals, but a simple laminated structure.

The great extinct Megatherium possessed a dentine which

(¹) Outer layer of the dentine of a cod.

was very rich in vascular canals, but their arrangement was a little different from that just described, as may be seen in the figure, to the left of which lies the inner portion of the dentine, very rich in vascular canals; this merges into a fine tubed dentine, the vascular canals all ending at the same distance from the surface, while outside this again comes the very vascular cementum.

Fig. 40 (¹).

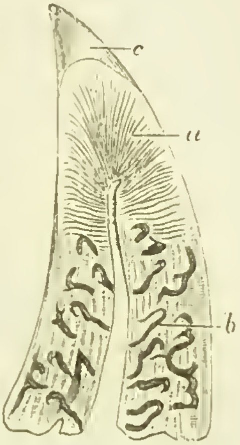
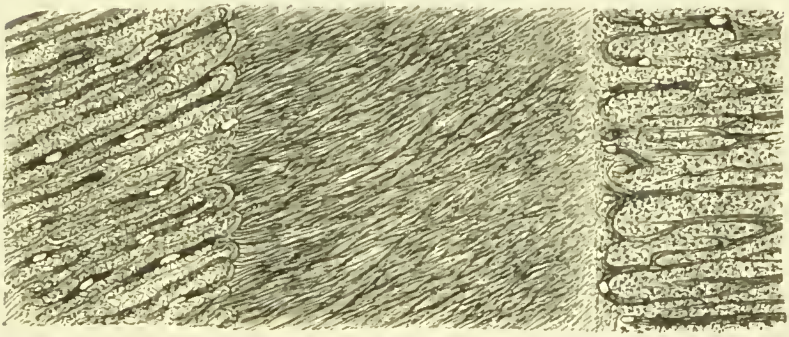


Fig. 41 (²).



The typical vaso-dentine teeth appear to be a good deal

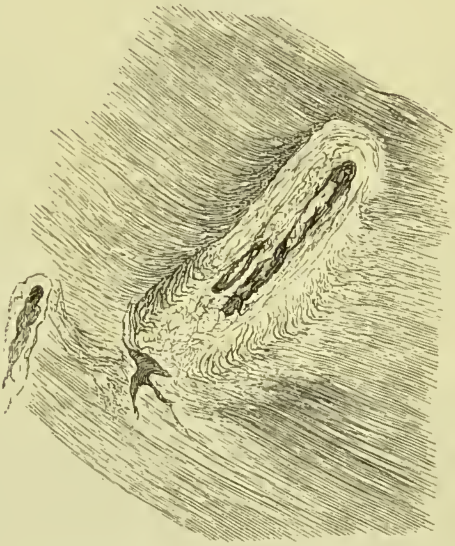
(¹) Tooth of flounder. *a.* Hard dentine. *b.* Vascular canals. *c.* Enamel tip. For other examples of vaso-dentine, see the figures of the teeth of Chætodon, of Odontostomus, &c.

(²) Dentine and cementum of Megatherium; the latter lies to the right.

softer than those which are composed of fine tubed dentine, and accordingly they are generally either completely coated, or at all events tipped with enamel.

It occasionally occurs that a vascular canal persists in the hard dentine of a human tooth; in such cases there is no relation between these canals and the course of the dentinal tubes, the latter being, as is seen in Fig. 42, which was drawn from a specimen shown to me by Dr. Andrews at Cambridge, Massachusetts, displaced from their course by it.

Fig. 42 (1).



These canals, which occasionally occur both in human and other mammalian teeth, are to be regarded quite as abnormalities, but there is yet another modification of vascular canal which occurs as an invariable character in certain teeth, and which is of great interest from the point of view of evolution, since it exemplifies vascular canals losing their function and in process of disappearance. Towards the base of the teeth of Sargus, for instance, loops of uniform calibre, with their concavities directed towards the pulp, may be seen; no one familiar with the canals of vaso-dentine can for a moment doubt that they were formed around a vessel, but though such was their origin, the vessel soon ceased to be pervious, and their open ends stop far short of the pulp chamber, in the midst of the dentine.

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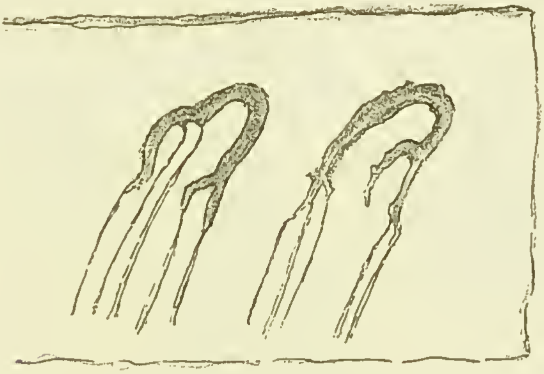
(1) Vascular canal in human dentine.

And it is interesting to note that their ends are not abruptly cut off and sealed, but that they taper down and are continuous with one, two, or three dentinal canals. (Fig. 43.)

Nothing is known of the contents of these loops in the fresh tooth, but it hardly admits of doubt that this partial persistence of the vascular channel, speedily abandoned in the further building of the dentine, indicates descent from a form in which these canals were functional, and the type of dentine a real vaso-dentine. The walls of these canals are smooth, just as in a typical vaso-dentine, but there is yet another form of canal in which it has departed a little more from its pristine type.

Fig. 43 (1).



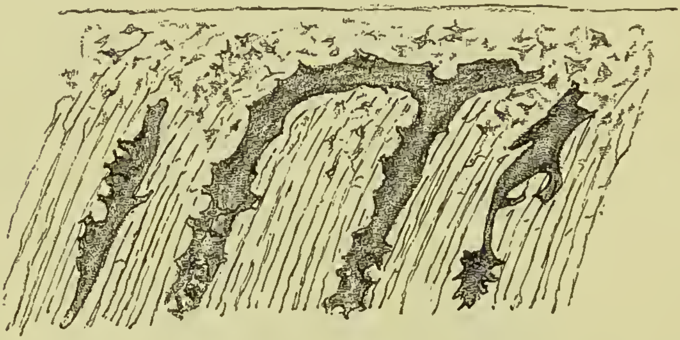
In the outer part of the dentine of the Manatee a series of regular loops are to be seen, which at first sight look like, and in the earlier editions of this book were described as, vascular canals. Just as in Sargus, their general arrangement, their fairly uniform diameter, &c., lead us to the conclusion that they mark the site of former vessels.

(1) Vascular loops from tooth of Sargus.

But in place of their interior being smooth, a higher power discloses that it has numerous irregular sharp prolongations running out from it, between which rounded projections encroach upon its lumen.

In point of fact the walls bounding the canal strikingly recall the walls of an interglobular space, and the whole canal might appropriately be compared to an enormously elongated interglobular space. As in Sargus, nothing is known of the contents in the fresh state; but as in that fish, it is hardly possible to doubt that we have before us the evidence that in some ancestral form there was a circulation through these channels.

Fig. 44 (¹).



The method of their disappearance is interesting; the dentinal tubes run into or past them, and had calcification gone a little farther, to the obliteration of our so-termed long interglobular space, the last trace of the ancestral vaso-dentine would have been gone.

OSTEO-DENTINE.

Osteo-dentine.—This is a tissue which in its most typical form is marked off from hard dentine, vaso-dentine, and plici-dentine alike by certain structural peculiarities and by the method of its development; and it sometimes approaches very

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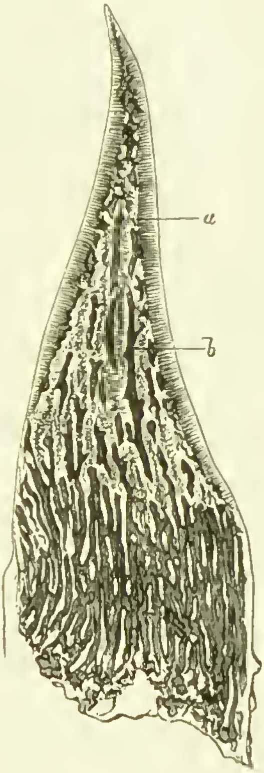
(¹) Dentine of Manatee. Showing partial persistence of vascular canals.

nearly to bone, from which indeed it has few essential points of difference. But there are many transitional forms, so that it is often hard to draw a sharp line of distinction between them.

The difference can hardly be fully appreciated until the development of dentine has been described; but it may be

FIG. 45 (1).



at once mentioned that osteo-dentine is not wholly formed upon the surface of the pulp, and it results from this that whereas the pulp chamber has a definite outline in those forms thus far described, and the pulp can be bodily pulled out, in osteo-dentine calcified trabeculæ shoot right through the pulp, there is ultimately no sharply defined pulp chamber, and the pulp cannot be pulled out, the pulp and the hard tissues being inextricably mixed up.

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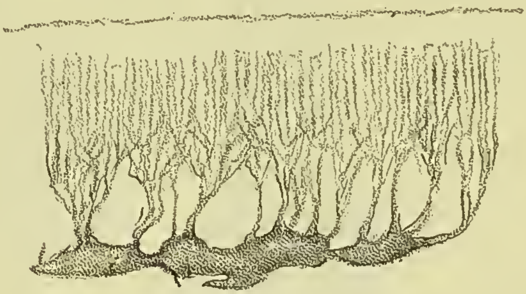
(1) Tooth of common pike. *a.* Outer layer of fine tubed dentine; *b.* inner mass of osteo-dentine.

And though there are numerous large channels, often much larger than those of vaso-dentine, they are less regular, do not in their arrangement so closely follow the form of capillary loops, and in a fresh tooth contain masses of pulp-structure as well as blood-vessels.

The pike's tooth affords a good example of osteo-dentine. Its surface is formed of a layer of fine tubed tissue, almost like ordinary dentine, but this soon gives place to a coarsely channelled tissue, containing elongated spaces filled with pulp, from which canaliculi, like those of a bone lacuna, branch off in all directions, but do not run far.

Fig. 46 (1).



The fine tubed layer which forms the exterior differs from ordinary dentine in the respect that the tubes, although parallel in their outer portion, in the absence of a general pulp cavity as they pass inwards become gathered together into fewer and larger tubes, which again originate from the somewhat irregularly shaped channels in the interior of the tooth.

Their relationship to the fine tubes which occur in less abundance in the deeper parts of the tooth is thus shown, and the close resemblance of these dentinal tubes to the canaliculi of ordinary bone becomes apparent.

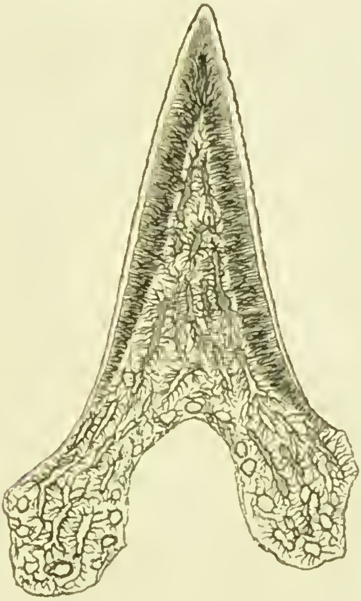
It is stated by Sternfeld ("Archiv. f. Mick. Anat.," Bd. 20)

(1) Outer layer of the dentine of the tooth of a pike. The fine canals are seen to be gathered into bundles, which spring from the large canals of the axial portion of the tooth.

that flattish cells line all the surfaces, and that processes from these enter the tubes.

The structure of the teeth of sharks shows a large amount of variability; thus the teeth of the great white shark (Carcharias), which is so formidable in the tropics, are composed of ordinary fine tubed dentine, with the exception of their bases, which are of osteo-dentine.

Fig. 47 (¹).



On the other hand, the teeth of the Porbeagle shark (Lamna) consist of a central core of osteo-dentine surrounded with (?) enamel. In the former editions of this book this was described as an outer layer of fine tubed dentine, its structure suggesting this. But more careful observations show by comparison with other forms, as well as by a more critical examination of the tissues itself, that this is an entirely peculiar tissue, and that the osteo-

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(¹) Tooth of a species of Lamna, consisting of a central mass of osteo-dentine, passing towards its surface into a fine-tubed unvascular dentine. The clear structureless layer on the surface may probably be regarded as enamel.

dentine core has a fine tubed outer layer, but it is not in all respects like that described in the pike. (Cf. p. 31).

In the osteo-dentine medullary canals of varying size run, with a direction, roughly speaking, parallel to the long axis of the tooth, anastomosing with one another, and from their sides wavy bundles of fine tubes radiate, but do not run far; that is to say, its dentinal tubes do not radiate from any one central pulp chamber, but from an indefinitely large number of canals.

Where, as happens in some sharks, these medullary canals are very regular in size, are placed at nearly uniform distances from each other, and run parallel with one another towards the surface, we have a structure not widely different from that found in Myliobates or in Pristis, which might almost be described as an osteo-dentine of abnormal regularity, in which the tube system had attained an unusual degree of development.

At the other extremity of the series we find canals much more branched and irregular in their course than in Lamna, the tubes radiating from them reduced in amount and extent, some degree of lamination of the matrix, and, in fact, a tissue which is practically like ordinary bone.

The similarity of the channels of pulp in osteo-dentine to Haversian canals in bone is very close; in fact, when teeth consisting of osteo-dentine become, as in many fish they do, anchylosed to the subjacent bone, it becomes impossible to say at what point the dentine ends and the bone commences; and this difficulty is intensified by the fact that the bone of many fishes lacks lacunæ, and is almost exactly like dentine. In fact, in many fish the outer compact layer of the jaw-bone has fine parallel canaliculi, and no other structure is visible, so that it bears a close resemblance to the external layer of these osteo-dentine teeth.

Osteo-dentine was defined by Professor Owen as dentine in which the matrix was arranged in concentric rings around the vascular canals, and in which lacunæ similar to those of bone were found.

But neither of these characters are to be found in many teeth, which, if the manner of their development is to be taken into account, are unquestionably made of osteo-dentine; and so they cannot be made use of for purposes of definition, although lacunæ and lamination of the matrix are far more often present in osteo-dentine than in the other varieties of dentinal structure.

It will be seen from what has gone before that the varieties of dentine run into one another, and it becomes a matter of difficulty to frame satisfactory definitions, especially in the case of osteo-dentine, without taking into account its development.

The varieties of dentine may be grouped thus :—

(A.) Dentines developed upon the surface of a pulp, by calcification of its surface layers. Dentinal tubes, when present, radiating from a single axial pulp chamber.

- (i.) Hard, unvascular dentine, thoroughly permeated with dentinal tubes, which radiate from a simple central pulp chamber. Example—Human dentine.
- (ii.) Plici-dentine, permeated with dentinal tubes, which radiate from a pulp chamber rendered complex in form by foldings in of its walls. Example—Lepidosteus, Labyrinthodon.
- (iii.) Vaso-dentine, with dentinal tubes few or absent, but capillary channels with blood circulating through them abundant. Example—Hake.
- (iv.) Dentines which might be regarded as aggregations of fused parallel denticles, as forms of folded dentine, or as transitional towards a very regular osteo-dentine. Example — Myliobates, Pristis.

(B.) Dentines developed by calcification shooting through the interior of a pulp, not by calcification of a surface layer. Dentinal tubes have relation to the medullary tracts left, and not to an axial pulp chamber.

(v.) Osteo-dentine; with dentinal tubes which radiate from numerous medullary channels, and which may be only short and few in number, or may be fully developed. Lamination of the matrix and spaces like bone lacunæ occur in some osteo-dentines. Example—Pike, Lamna.

It remains to be added that the same pulp may undergo a change in the manner of its calcification; that is to say, that after having gone on with surface calcification for a certain length of time, this may give place to a more irregular internal calcification into an osteo-dentine.

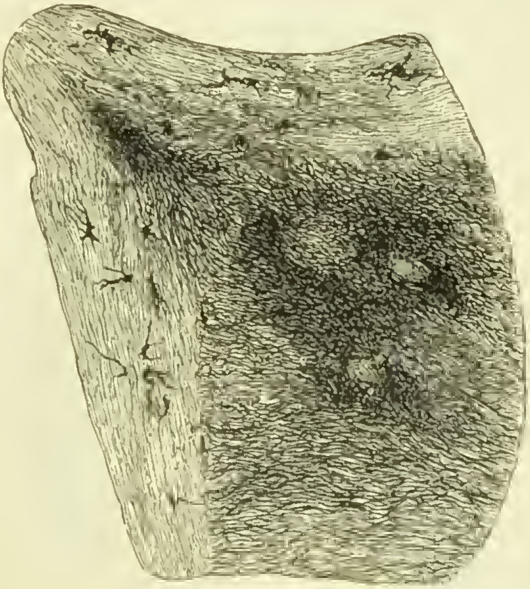
This is especially prone to happen after injury, and is often exemplified upon a large scale in elephants' tusks; the pulps of which, normally engaged in calcifying the odontoblast layers into ivory, may after an injury calcify irregularly, and solidify into a coarse osteo-dentine.

It will then be easy to understand that so-called secondary dentine, produced in a pulp which ordinarily forms hard dentine, may partake of the character of hard, of vaso-, or of osteo-dentine.

Thus the pulp of a sperm whale's tooth becomes obliterated by a development of secondary dentine, which sometimes forms irregular masses loose in the pulp chamber, and sometimes is adherent to and continuous with the dentine previously formed. The structure of these masses is very confused. Tubes, of about the same diameter as dentinal tubes, abound; but they are often arranged in tufts or in bundles, and without any apparent reference to any common points of radiation. Irregular spaces, partaking of the character of interglobular spaces or of bone lacunæ, abound; and vascular canals are also common.

In the human tooth secondary dentine occurs in the teeth of aged persons, in which the pulp cavity is much contracted in size, and is also very frequently formed as a protection to the pulp when threatened by the approach of dental caries, or by the thinning of the walls of the pulp cavity through excessive wear. The accompanying figure, representing one of the cornua of the pulp chamber from a molar tooth affected by caries, is a good example of secondary dentine. It occasionally happens that the pulp resumes its formative activity, and new dentine is developed, which, with the exception of a slight break or bend in the continuity of the tubes, is almost exactly like normal dentine. More often, however, the boundary line between the old and the new is marked by an abundance of irregular spaces and globular contours, whilst further in the mass of new secondary dentine the tubular structure again asserts itself more strongly: this is well seen in the specimen figured.

Fig. 48 (1).



The axial portions of many teeth of persistent growth, for some little distance below the working surfaces, become filled by a calcification which has much in common with the secondary dentines—that is to say, it is of coarser and less definite structure than the peripheral parts of the same tooth.

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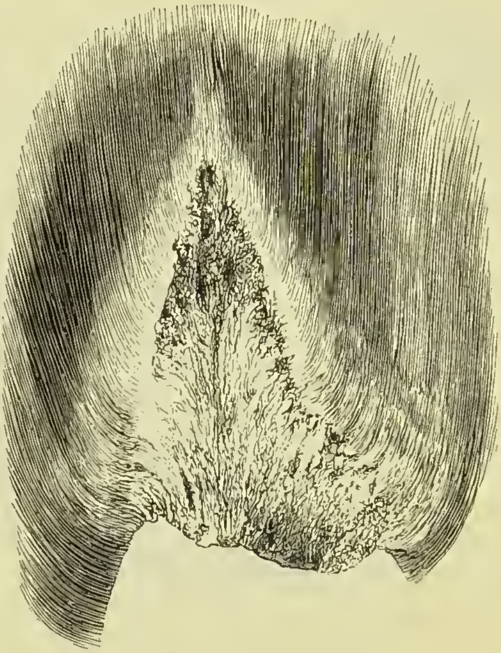
(1) Section of a mass of secondary dentine from the tooth of a sperm whale.

For example, in the armadillo the axial portion of the tooth is made up of a tubular tissue, but the tubes are crowded together into irregular bundles, and instead of running from the interior towards the surface, they run more or less along the axis of the tooth. In another member of the Edentata (the sloth) the axial portion differs much more from the outside, being very much softer and more porous, containing, in fact, a large number of vascular channels, and being very apt to break away in the process of rubbing down the section.

Fig. 49 (1).



Amongst Rodents the final closure of the axial tract takes place in some almost by a continuance of the formation of fine tubed dentine, with a very small amount of secondary dentine, while in others there is a large area of dentine with vascular tracts in it. In the persistently growing incisor of the kangaroo there is a mass of secondary dentine which is sometimes almost glassy looking and structureless. In some specimens of secondary dentine from an elephant's tusk Mr. Mummery found an abundant connective tissue stroma after decalcification.

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(1) Secondary dentine filling up one of the cornua of the pulp cavity From a human molar affected by caries.

CHAPTER III.

THE TOOTH PULP.

THE pulp occupying the central chamber or pulp cavity was the formative organ of the dentine, and consequently varies in its anatomical characters according to its age. As well as being what remains of a formative organ, it is the source of vascular and nervous supply to the dentine.

The pulp may be described as being made up of a very delicate connective tissue with large spaces filled with a jelly-like material, the fibres of which are probably the processes of the cells. The cells are fairly abundant and are dispersed throughout it. Some ordinary fibrous connective tissue is discoverable in it. Nerves and vessels also ramify abundantly in it.

The matrix substance remaining in large proportion, whilst the cells and their products are not greatly developed, and the fibrous element being still less conspicuous, gives to the pulp a character common to many embryonic tissues. At an early period the dentine papilla consists wholly of roundish embryonic cells, a surface layer of specialised cells, the future odontoblasts, soon making their appearance.

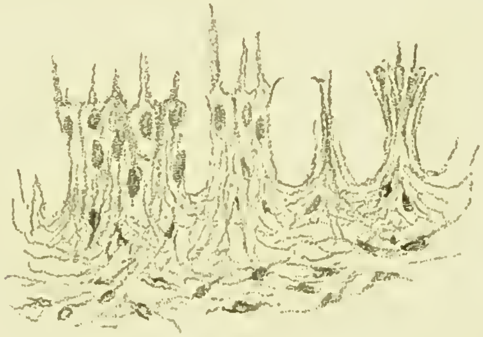
The deeper cells grow out into processes, but these remain very fine, and at no period are there large bundles of connective tissue fibres to be found unless the pulp has undergone degeneration in advanced age.

In a specimen cut from a loose tooth in an aged person, which was lent to me by Mr. Hopewell Smith, the cell elements have all completely disappeared, and there remains nothing but connective tissue, the bundles of which run into the dentine. It is possible that the conspicuousness of this connective tissue may partly be due to the fact that it is in no degree concealed by the abundant cells of an ordinary pulp, but it seems probable that the connective tissue itself is also coarser and more abundant.

The cellular elements of the pulp are arranged, as seen in transverse sections, in a direction radiating outwards from the centre; this is most marked in the highly specialised layer of cells which form the surface of the pulp, and are termed *odontoblasts.*

The odontoblast layer, sometimes called the *membrana eboris*, because it usually adheres more strongly to the dentine than to the rest of the pulp, and is therefore often left behind upon the dentine when the pulp is torn away, consists of a single row of large elongated cells, of darkish granular appearance, with a large and conspicuous nucleus near to the end farthest from the dentine.

FIG. 50 (¹).



The sharp contours which the odontoblasts possess in pulps which have been acted on by chromic acid, alcohol, or even water, are absent in the perfectly fresh and unaltered condition, and it is believed that they have no special investing membrane. They are furnished with three sets of processes. The *dentinal process* (which is equivalent to the dentinal fibre) enters the canal in the dentine, and the individual odontoblasts may be furnished with several dentinal pro-

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(¹) Surface of human pulp, showing odontoblasts with their processes.

cesses. By means of *lateral processes* the cells communicate with those on either side of them, and by means of their *pulp processes* with cells lying more deeply. The process which enters the dentinal tubes is of some size, tapers a little, and sticks out from the cell so straightly that it appears to be somewhat stiff.

Dr. Aitchison Robertson describes the pulp process in the odontoblasts of the ox as being very long and fine, but says that there is no lateral union: his specimens, however, appear to have been mostly teased out.

The membrana eboris covers the surface of the pulp like an epithelium. The odontoblasts vary much in form at different periods; in the youngest pulps, prior to the formation of dentine, they are roundish, or rather pyriform; during the period of their greatest functional activity the end directed towards the dentine is squarish, though tapering to a slight extent into the dentinal process; while in old age they become comparatively inconspicuous, and assume a rounded or ovoid shape. The odontoblasts in hardened sections are often slightly separated from one another, an effect which is rarely seen in the enamel cells—a fact which would indicate either that they have no definite limiting membranes, or else that they are of a softer material. They generally, however, adhere together firmly at their ends which are nearest to the dentine, so as to form here a continuous sheet. The general matrix of the pulp, as has been before noted, is of firm, gelatinous consistency; it is a little more dense upon the surface, whence has perhaps arisen the erroneous idea that the pulp is bounded by a definite membrane.

The vessels of the pulp are very numerous; three or more arteries enter at the apical foramen, and, breaking up into branches which are at first parallel with the long axis of the pulp, finally form a capillary plexus immediately beneath the cells of the membrana eboris.

No lymphatics are known to occur in the tooth pulp.

The nerves enter usually by one largish trunk and three or four minute ones: after pursuing a parallel course, and giving off some branches which anastomose but little in the expanded portion of the pulp, they form a rich plexus beneath the membrana eboris, as has been described by Raschkow and many subsequent writers.

But here our exact knowledge ends, for the nature of the terminations of the nerve fibres in the pulp is not with certainty known: the primitive fibrils, which are extraordinarily abundant near to the surface of the pulp, often form meshes, but this does not appear to be their real termination.

Boll, as has been mentioned at a previous page, investigated this point, and found that if a pulp be treated for an hour with very dilute chromic acid solution, an immense number of fine non-medullated nerve fibres, which he succeeded in tracing into continuity with the larger medullated fibres, may be discerned near to the surface of the pulp. The ultimate destination of these nerve fibres is uncertain; but he has seen them passing through the membrana eboris, and taking a direction parallel to that of the dentinal fibrils in such numbers that he infers that they have been pulled out from the canals of the dentine. Still, whatever may be the probabilities of the case, he has not seen a nerve fibre definitely to pass into a dentinal canal, nor has any other observer been more fortunate.

Boll's observations have not however been fully confirmed by any subsequent worker in the field, nor have they been definitely controverted until Magitot recently stated that he had fully satisfied himself that the nerves become continuous with the branched, somewhat stellate, cells which form a layer beneath the odontoblasts, and through the medium of these cells with the odontoblasts themselves. (See Fig. 25.)

If this view of their relation to the nerves be correct the sensitiveness of the dentine would be fully accounted for without the necessity for the supposition that actual nerve fibres enter it, for the dentinal fibrils would be in a measure themselves prolongations of the nerves.

Mr. Mummery, using as a stain an iron salt followed by tannin, has succeeded in showing that from the nerve bundles which course along more or less parallel with the surface of the pulp very fine fibres are given off, which run up to the dentine.

There is every appearance of their entering it, but such is the difficulty of the investigation where very delicate structures are in relation with a calcified material that no absolute certainty has been arrived at with respect to them. It will hence be seen that some uncertainty still attaches to the odontoblasts and their function, but to this it will be necessary to recur in treating of the development of the dentine.

This difference of opinion as to the function of the odontoblast cells never can be finally settled until the nerve-endings of the pulp are clearly demonstrated. The idea that the odontoblasts themselves are nerve-end organs was advocated by Mr. Coleman, and more recently by Mr. Hopewell Smith ("Trans. Odontol. Soc.," 1893); but there are many objections to this view, amongst others being the occurrence of well-marked odontoblasts in places where they seem not only useless but decidedly misplaced as nerve-end organs.

Dr. Robertson ("Trans. Roy. Soc. Edinb.," 1891) describes the nerves of the tooth pulp of the ox, his specimens mostly having been made by teasing fresh pulp in 1 per cent. solution of osmic acid. He describes large bundles of medullated and non-medullated fibres, the former being the more numerous, and in the teased specimen the axis-cylinder of medullated fibres was often seen stretching far beyond the sheath. He believes that the axis-cylinders of medullated nerves lose their sheath, and after running for a greater or less distance, become continuous with the pulp process of the odontoblasts, which therefore, with their dentinal processes, become nerve-end organs, so that he so far agrees with Magitot.

Towards the outer surface of the pulp, but inside the odontoblasts, Weil has described a layer about which there has been, and indeed still is, some controversy. It goes by the name of the "basal layer of Weil," and consists of a comparatively pale and transparent zone lying between the inner ends of the odontoblasts and the deeper part of the pulp. He describes it as consisting of fine connective tissue fibres which communicate with the processes of the odontoblasts. Mr. Mummery points out that though visible in many of his preparations made by Weil's (Koch's) process, it is absent near to the growing base of young teeth, and it is in the crown that it is most pronounced. He disagrees with Weil as to the connection of the fibres of this layer with the odontoblasts, saying that he has often traced these fibres through the cell layer into the dentine matrix. Von Ebner altogether doubts its existence, attributing it to the pulp shrinking back while the odontoblasts are held up to the dentine by their processes. Röse shares Von Ebner's view. Weil compares it to a basement membrane, urging that a fibrillar structure has been detected in many undoubted basement membranes, but whether it be a real normal or an artificial structure, there seems little reason to regard it as anything more than connective tissue pulp stroma.

It has already been mentioned that the pulp undergoes alterations in advanced age, its diminution in size by its progressive calcification and the addition thus made to the walls of the pulp cavity being the most conspicuous changes which occur. In pulps which have undergone a little further degeneration, the odontoblast layer becomes atrophied; fibrillar connective tissue becomes more abundant, coincidently with the diminution in the quantity of the cellular elements. Finally, the capillary system becomes obliterated by the occurrence of thrombosis in the larger vessels, the nerves undergo fatty degeneration, and the pulp becomes reduced to a shrivelled, unvascular, insensitive mass.

These changes may go on without leading to actual putrefactive decomposition of the pulp, and are hence not attended by alveolar abscess; but a tooth in which the pulp has undergone senile atrophy is seldom fast in its socket.

The pulps of the teeth of some animals become eventually entirely converted into secondary dentine, but it would seem to be very generally the case that those teeth which exercise very active functions and last throughout the life of the creature retain their pulp in an active and vascular condition.

CEMENTUM.

The cement forms a coating of variable thickness over the roots of the teeth, sometimes, when the several roots are very close to one another, or the cement is thickened by disease, uniting the several roots into one.

The cement is ordinarily said to be absent from the crowns of the teeth of man, the carnivora, &c., and to commence by a thin edge just at the neck of the tooth, overlapping the enamel to a slight extent; it is, in the healthy state, thickest in the interspaces between the roots of molar or bicuspid teeth; it is, however, often thickened at the end of a root by a dental exostosis. In compound teeth, the cementum forms the connecting substance between the denticles (see the figures of the tooth of the Capybara, the Elephant, &c.), and, before the tooth has been subject to wear, forms a complete investment over the top of the crown. The cementum also covers the crowns of the complex-patterned crowns of the teeth of ruminants. The cementum is the most external of the dental tissues: a fact which necessarily follows from its being derived more or less directly from the tooth follicle.

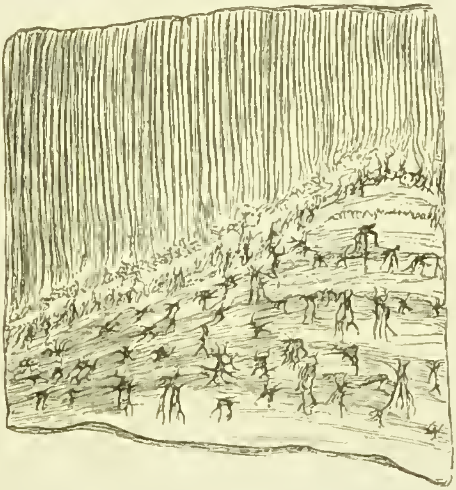
Both physically and chemically, and also in respect of the manner of its development, the cementum is closely allied to bone. It consists of a laminated calcified matrix or basal substance, and lacunæ. Vascular canals corresponding to the Haversian canals of bone are met with, but it is only in thick cementum that they exist; and, in man, perhaps in exostosis more often than in the thick healthy tissue.

The lamellæ of the cementum are thinner towards the neck of the tooth, being thickest at the apex of the root, but the number of the lamellæ is about the same in all parts of the tooth.

Soon after the completion of a tooth, there are but few lamellæ, so that an adult has cementum far thicker than a child; an aged person again having more than an adult. Very possibly it is to be regarded as growing at intervals through the life of the individual (Black).

The matrix is a calcified substance, which, when boiled, yields gelatine, and if decalcified retains its form and structure: it is, in fact, practically identical with the matrix of bone. It is sometimes apparently structureless, at others finely granular, or interspersed with small globules.

Fig. 51 (1).



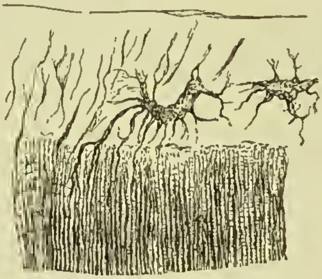
The lacunæ of cementum share with those of bone the following characters: in dried sections they are irregular cavities, elongated in the direction of the lamellæ of the matrix, and furnished with a large number of processes. The processes of the lacunæ (known as canaliculi) are most abundantly given off at right angles to the lamellæ (see Fig. 51), and, again, in cementum, are more abundantly directed towards the exterior of the root than towards the dentine. The lacunæ of cementum differ from those of

(1) Thick laminated cementum from the root of a human tooth.

bone in being far more variable in size, in form, and in the excessive number and length of their canaliculi; in this latter respect the lacunæ of the cement of Cetacean teeth are very remarkable.

Many of the lacunæ in cementum are connected, by means of their canaliculi, with the determinations of the dentinal tubes (Fig. 52); they, by the same means, freely intercommunicate with one another, while others of their processes are directed towards the surface, which, however, in most instances, they do not appear to actually reach.

FIG. 52 (1).



The lacunæ assume all sorts of peculiar forms, especially in the thicker portion of the cement.

Here and there lacunæ are to be found which are furnished with comparatively short processes, and are contained within well-confined contours. Sometimes such a line is to be seen surrounding a single lacuna, sometimes several lacunæ are enclosed within it; lacunæ so circumscribed are called "encapsuled lacunæ," and were first observed by Gerber in the cement of the teeth of the horse (they are specially abundant in the teeth of the Solidungulata). By cautious disintegration of the cementum in acids these encapsuled lacunæ may be isolated: the immediate walls of the lacunæ and canaliculi, just as in bone, being composed of a material which has more power of resisting chemical reagents than the rest of the matrix.

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(1) Lacuna of cementum which communicates with the terminations of the dentinal tubes.

The encapsuled lacunæ are to be regarded as individual osteoblasts, or nests of osteoblasts, which have to some extent preserved their individuality during calcification.

In the fresh condition it appears probable that the lacunæ are filled up by soft matrix, which shrinks, and so leaves them as cavities in dried sections. It can hardly as yet be said that the question of the contents of lacunæ has been finally settled, though the researches of Bödecker and Heitzmann have gone far towards doing so.

According to them each lacuna contains a protoplasmic body, which they term the cement corpuscle, with a central nucleus.

This nucleus may be large and surrounded by but little protoplasm, or it may be small; or there may be many nuclei.

Dr. Heitzmann, after staining with gold chloride, claims to have demonstrated protoplasmic matter in the thin layer of cementum of the neck of the tooth, and while I by no means go with him in regarding everything which will stain with chloride of gold as protoplasm, yet clinically there is no doubt, or very little, that the cementum in this locality is very sensitive, and that there is an *à priori* probability that there is some uncalcified tissue there. At the same time it must be remembered that half-calcified tissue can be stained with silver nitrate, and sometimes also with gold, on the periphery of the pulp, in interglobular spaces, and in Neumann's sheaths, and one would quite expect to find in the interstices of the globular forms that can be made out in this thin cementum layer such half-calcified matrix material.

Dr. Heitzmann also throws doubt upon the perforating fibres that have been described being Sharpey's fibres; he interprets them also as protoplasmic.

The cement corpuscles communicate freely with one another by offshoots, those of large size occupying the conspicuously visible canaliculi of the lacunæ, whilst the finer offshoots are believed by Heitzmann to form a delicate network through the whole basis substance or matrix. The cement corpuscles near to the external surface give off numerous offshoots which communicate with protoplasmic bodies in the periosteum. By this means the cementum can remain alive even when the pulp of the tooth is dead, and thus the tooth be in no way a mere foreign body, dead and inert.

Like bone, cementum contains Sharpey's fibres; that is to say, rods running through it at right angles to its own lamination, and, as it were, perforating it. These are probably calcified or uncalcified bundles of connective tissue. And it is by the medium of these that the alveolo-dental periosteum adheres to the cementum.

Where the cementum is very thin, as, for instance, where it commences at the neck of a human tooth, it is generally to all appearance structureless, and does not contain any lacunæ and therefore no protoplasmic bodies: nevertheless, lacunæ may be sometimes found in thin cementum, as, for example, in that thin layer which invests the front of the enamel of the rodent-like tooth of a wombat.

The cementum at the neck is also devoid of lamellæ; it appears to be built up by direct ossification of osteoblasts, the prismatic shape of which may be traced in it; Bödecker describes it as permeated by a fine but abundant network of soft living matter. The larger dentinal tubes fall short of the boundary line at the neck, but according to him a fine protoplasmic network crosses it. He states that it has a covering of epithelial elements, like those of the gum.

The outermost layer of thick cementum is a glassy film, denser apparently than the subjacent portions, and quite devoid of lacunæ; on the surface it is slightly nodular, and might be described as built up of an infinite number of very minute and perfectly fused globules; this is, in fact, the youngest layer of cement, and is closely similar to that globular formation which characterises dentine at an early stage of its development.

The cementum is very closely, indeed inseparably, connected with the dentine, through the medium of the "granular" layer of the latter; the fusion of the two tissues being so intimate that it is often difficult to say precisely at what point the one may be said to have merged into the other. And in this region there is an abundant passage of protoplasmic filaments across from the one to the other.

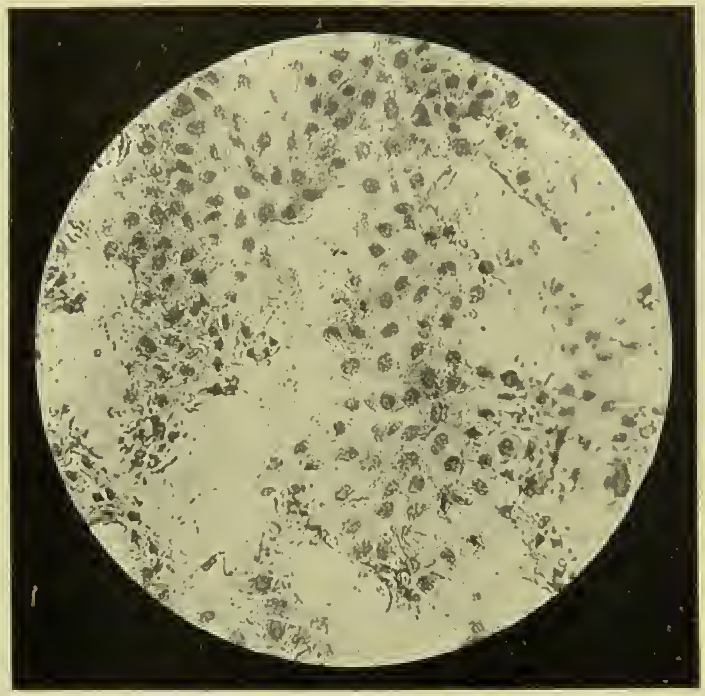
Nasmyth's membrane.—Under the names of Nasmyth's membrane, enamel cuticle, or persistent dental capsule, a structure is described about which much difference of opinion has been, and indeed still is, expressed. Over the enamel of the crown of a human or other mammalian tooth, the crown of which is not coated by a thick layer of cementum, there is an exceedingly thin membrane, the existence of which can only be demonstrated by the use of acids, which cause it to become detached from the surface of the enamel. When thus isolated it is found to form a continuous transparent sheet, upon which, by staining with nitrate of silver, a reticulated pattern may be brought out, as though it were made up of epithelial cells. It is exceedingly thin, Kölliker attributing to it a thickness of only one twenty-thousandth of an inch, but, nevertheless, it is very indestructible, resisting the action of strong nitric or hydrochloric acid, and only swelling slightly when boiled in caustic potash. Notwithstanding, however, that it resists the action of chemicals, it is not so hard as the enamel, and becomes worn off tolerably speedily, so that to see it well a young and unworn tooth should be selected.

The singular power of resistance to re-agents which characterises it proves nothing more than that it is a tissue, imperfectly calcified, on the border-land of calcification, so to speak, since similarly resistant structures are to be found lining the Haversian canals, the dentinal tubes, the surface of developing enamel, the lacunæ, &c. When burnt it gives off a smell like that of burning horn.

In my father's opinion ("Dental Surgery," 1859) it was to be regarded as a thin covering of cementum, and I gave additional evidence in support of this view in a paper referred to in the list of works which follows this chapter.

The more recent investigations of Dr. Paul ("Dental Record," 1896) have, however, thrown a fresh light upon the matter, and have shown that the points upon which I chiefly relied are susceptible of quite a different explanation. He took unworn teeth, hardened them in a chromate solution, and lifted the membrane by a five per cent. solution of nitric acid; he has since simplified the process by decalcifying the enamel at once by immersion in a phloroglucin decalcifying solution without the preliminary hardening.

FIG. 53 (1).



The detached membrane was stained in eosin or in Ehrlich's acid hæmatoxylin, washed, and mounted in Farrant's medium.

This at once shows the reticulated pattern; but that this is not due to the impressions of the ends of the enamel prisms is proved by its being too large—ten times too large according to Dr. Paul—and, in addition, there are large nuclei which are so related to the pattern as to show that it is produced by the margins of the cells of which they are the nuclei. His specimens, from one of which the appended figure is taken, leave no doubt but that it is a membrane composed of a layer of flat epithelial cells.

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(1) Nasmyth's membrane, showing the stained nuclei. From a specimen prepared and photographed by Dr. Paul.

It is obvious that a layer of flat epithelial cells in this situation can have only one source, namely, some part of the enamel organ, and Dr. Paul found that in cutting sections of the dental sac he was able to find upon its inner surface a layer of flat epithelial cells, which could be traced to be the external epithelium of the enamel organ. Hence the present state of knowledge on the subject must lead us to the conclusion that Waldeyer was right, and that Nasmyth's membrane is a product of the external layer of the enamel organ.

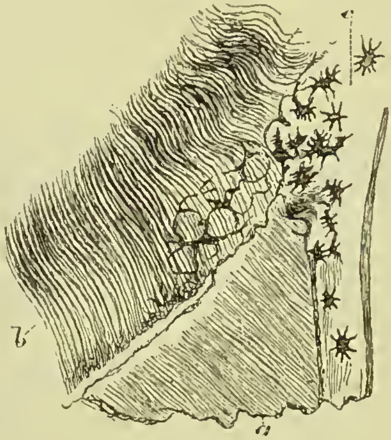
In addition to the layer of epithelial cells, there appears to be a thin structureless membrane inside them, *i.e.*, between them and the enamel, which is of such consistence as to make the isolated Nasmyth's membrane tend to curl up. Upon the inner surface of this membrane the pitted impressions of the ends of the enamel prisms may sometimes be seen, as described by the older observers.

Like the epithelial layer, this membrane must, from its position, be a product of the enamel organ. Dr. Paul suggests that it may be of some service in protecting the enamel by its power of resistance to acid, especially in those depressions which are the most vulnerable points in a tooth, from which it would not get worn off as it does from the more exposed regions.

Other views have been held as to the nature of Nasmyth's membrane. It has been thought (1) to be a thin layer of cementum, too thin to show the characteristic structure of cementum, as supposed by my father and by myself; (2) to be a final product of the enamel cells or ameloblasts (Kölliker); (3) to be derived from the external epithelium of the enamel organ.

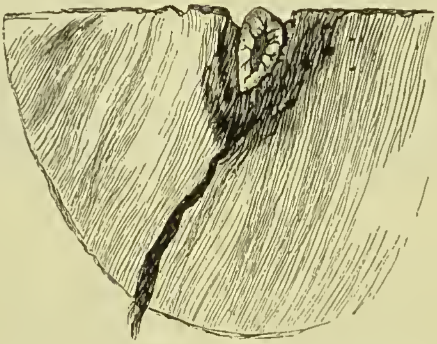
The grounds upon which I believed it to be a thin layer of cementum were that in a large number of animals there is a thick and functional layer of cementum outside the enamel, and that it now and then happens that the cementum upon a more or less abnormal human tooth, instead of coming to an end at the neck of the tooth, is continued up over the exterior of the enamel. This occurs less uncommonly than is generally imagined, and the accompanying figure represents a portion of the crown of such a tooth.

Fig. 54 (1).



If the section be made of the grinding surfaces of such teeth as present rather deep fissures, in these situations well marked and unmistakable lacunal cells, or encapsuled lacunæ, will be met with occasionally. Now and then an encapsuled lacuna may be found occupying a shallow depression in the enamel which it just

Fig. 55 (2).



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(1) From a section of bicuspid tooth in which the cementum, *c*, is continued over the outside of the enamel, *a*; the dentine is indicated by the letter *b*.

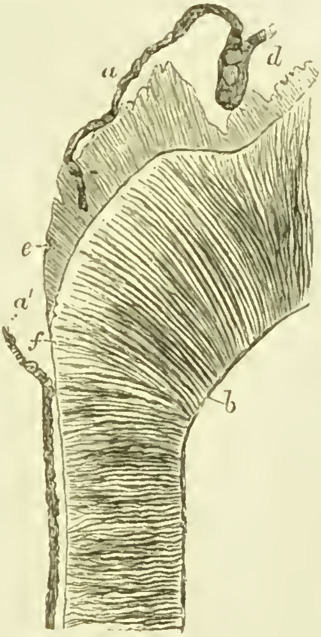
(2) Encapsuled lacuna occupying a pit in the enamel.

fits, but more commonly a dozen or more are crowded together in a pit in the enamel, where they are usually stained of a brownish colour. The occurrence of lacunæ in these situations is far from rare; my father's collection contains several good examples of them in these positions.

Nasmyth's membrane, thin though it is over the exterior of the enamel, is thickened when it covers over a pit or fissure, and when isolated by an acid is seen to have entirely filled up such spots (Fig. 56).

In these places, then, where the encapsuled lacunæ are to be found, Nasmyth's membrane also exists, a fact which alone would lend some probability to the view that it is cementum.

FIG. 56 (1).



The general absence of lacunæ in Nasmyth's membrane might have been due to the fact that it is not thick enough to contain them; just as the thinnest layers of unquestionable cementum also are without lacunæ.

In sections of an unworn bicuspid which was treated with acid subsequently to its having been ground thin and placed upon the slide, I have several times been fortunate enough to get a view of the membrane *in situ;* it then appears to be continuous with an exterior layer of cementum, which becomes a little discoloured by the acid employed to detach Nasmyth's membrane from the enamel. I was therefore inclined to regard it as young and incomplete cementum, and to consider it as representing (upon the human tooth) the thick cementum which covers the crowns of the teeth of Herbivora; and my friend Dr. Magitot, who has made many, as yet unpublished, researches upon this subject, entirely concurred in this view, which has also the support of Professor Wedl.

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(1) Nasmyth's membrane, set free by the partial solution of the enamel. *a.* Nasmyth's membrane. *b.* Dentine. *d.* Mass occupying a pit in the enamel. *c.* Enamel. *a'.* Torn end of Nasmyth's membrane.

It has however been pointed out by Dr. Paul that these observations are not inconsistent with the interpretation of its nature which he advocates, for the dental sac is present all over the crown of the tooth in man as well as in Herbivora, in which it does form coronal cementum; and it is quite possible that it might deposit encapsuled lacunæ in pits where there was room for them, and that these would appear to be in Nasmyth's membrane, which also goes into the pits; nor is its apparent continuity with the cementum at the neck more difficult to account for. To render the matter certain, Nasmyth's membrane should be demonstrated between the enamel and cementum in the teeth of Herbivora with thick coronal cement, but on this point Dr. Paul is not, as yet, prepared to speak with certainty.

Nasmyth, who first called attention to its existence, regarded it as "persistent dental capsule;" a view of its nature not very materially differing from that formerly advocated in these pages.

Professor Huxley described it as being identical with the membrana performativa; that is to say, with a membrane which covered the dentine papilla prior to the occurrence of calcification, and which afterwards came to intervene between the formed enamel and the enamel organ. The objections to the acceptance of this view of its nature are so inextricably wrapped up with other objections to Professor Huxley's theory of the development of the teeth that they cannot profitably be detailed in this place; it will suffice to say that evidence and the weight of authority alike point to there being no such true membrane as this membrana performativa in the place in question.

Waldeyer and Röse hold that it (*i.e.*, Nasmyth's membrane) is a product of a part of the enamel organ. After the completion of the formation of the enamel Waldeyer believes that the cells of the external epithelium of the enamel organ become applied to the surface of the enamel and there *cornify;* in this way he accounts for its resistance to reagents, and for its peculiar smell when it is burnt.

According to the statement of Dr. Magitot, the layer of cells in question (external epithelium of the enamel organ) is atrophied before the time of the completion of the enamel—a fact which, if confirmed, is fatal to Waldeyer's and Paul's explanation. This is a point which requires to be investigated afresh in the light of recent researches. Dr. Magitot, in his most recent paper on the subject ("Journal de l'Anatomie," &c., 1881), gives his adherence to the view that it is cementum.

Kölliker, who dissents strongly from the views of Waldeyer, and admits some uncertainty as to its nature, provisionally regards it as a continuous and structureless layer furnished by the enamel cells after their work of forming the fibrous enamel was complete; a sort of varnish over the surface, as it were.

THE GUM.

The gum is continuous with the mucous membrane of the inside of the lips, of the floor of the mouth, and of the palate, and differs from it principally by its greater density. Its hardness is in part due to the abundant tendinous fasciculi which it itself contains, in part to its being closely bound down to the bone by the blending of the dense fibrous fasciculi of the periosteum with its own. The fasciculi springing from the periosteum spread out in fan-like shape as they approach the epithelial surface. There is thus no very sharp line of demarcation between the gum and the periosteum when these are seen in section *in situ.*

The gum is beset with rather large, broad-based papillæ, which are sometimes single, sometimes compound; the epithelium is composed of laminæ of tesselated cells, much flattened near to the surface; but cylindrical cells form the deepest layer of the epithelium, the rete malpighi.

Small round aggregations of pavement epithelium are met with at a little depth, or even bedded in the surface; these, the "glands" of Serres, have no known function, but are remnants of the dental formative organs. In the neighbourhood of developing tooth-sacs epithelial aggregations of similar appearance are to be met with, and are remains of the dental lamina, which has undergone this curious change subsequently to the completion of its original function. The gums are rich in vessels, but remarkably scantily supplied with nerves.

At the necks of the teeth the gum becomes continuous with the periosteum of the internal surface of the alveoli, into which it passes without any line of demarcation.

THE ALVEOLO-DENTAL MEMBRANE.

The Alveolo-dental Periosteum, or Root Membrane, is a connective tissue of moderate density, devoid of elastic fibres, and richly supplied with nerves and vessels.

It is thicker near to the neck of the tooth, where it passes by imperceptible gradations into the gum and periosteum of the alveolar process, and near to the apex of the root. The general direction of the fibres is transverse; that is to say, they run across from the alveolus to the cementum, without break of continuity, as do also many capillary vessels; a mere inspection of the connective tissue bundles, as seen in a transverse section of a decalcified tooth in its socket, will suffice to demonstrate that there is but a single "membrane," and that no such thing as a membrane proper to the root and another proper to the alveolus can be distinguished; and the study of its development alike proves that the soft tissue investing the root, and that lining the socket, are one and the same thing: that there is but one "membrane," namely, the alveolo-dental periosteum.

At that part which is nearest to the bone the fibres are grouped together into conspicuous bundles; it is, in fact, much like any ordinary fibrous membrane. On its inner aspect, where it becomes continuous with the cementum, it consists of a fine network of interlacing bands, many of which lose themselves in the surface of the cementum.

But although there is a marked difference in histological character between the extreme parts of the membrane, yet the markedly fibrous elements of the outer blend and pass insensibly into the bands of the fine network of the inner part, and there is no break of continuity whatever.

The actual attachment, both to the cementum and to the bone, takes place by means of the connective tissue fibres, which pass right into the hard structures, which they traverse for some distance, and in this situation are known as Sharpey's fibres.

They pass through all the lamellæ of the cementum, and there are appearances of shrinkage in dry preparations which would lead to the inference that they were not very fully calcified ; in some portions of the cementum it seems to be almost composed of them, as at the neck of a tooth (Black). This writer states that they may be especially clearly seen in the pig, and that "they are the principal fibres of the peridental membrane included in the cementum in its growth, and furnish the means of making firm hold of the peridental membrane upon the root of the tooth. They are white connective tissue fibres, the ends of which are included in the matrix of the cementum sufficiently to make them apparent when the lime salts are removed, but when both are calcified, they cannot be demonstrated except in cases where there is imperfect calcification of the fibres, as has been mentioned above."

The thickness of the membrane appears to undergo a diminution with age, by calcification encroaching upon it from both the side of the bone and of the cementum.

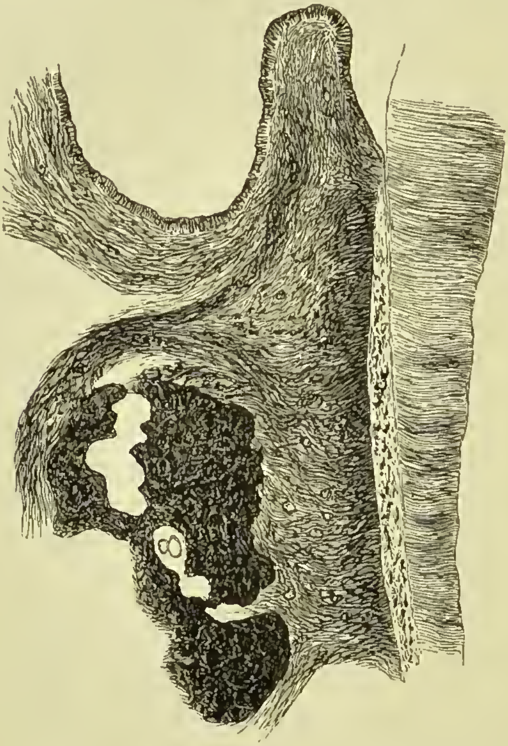
Malassez ("Archiv de Physiologie," 1885) urges that an ordinary periosteum in this situation would be too tender for the purposes of mastication, and that, as it is not a mere enveloping membrane, but is composed of fibrous bundles, which serve to sling the tooth in its place, it should be called the alveolo-dental ligament ; he further compares it with the fibrous bands which in some fishes serve to tie the tooth down to the bone where no tooth sockets exist, and holds that it is strictly homologous with these. Ranvier also points out that there is no isolable membrane such as there is on a long bone, and compares the alveolar cavity and its contents to a very large medullary space.

At the surface of the cementum it is more richly cellular, and here occur abundantly large soft nucleated plasm masses, which are the osteoblasts concerned in making cementum, and which by their offshoots communicate with plasm masses imprisoned within the cementum.

I have rarely seen the fibres, whether in longitudinal or in transverse sections, pass straight in the shortest possible line from the bone to the cementum, but they invariably pursue an oblique course, which probably serves to allow for slight mobility of the tooth without the fibres being stretched or torn.

The blood vessels are most abundant in membrane midway between the bone and the cementum, or rather nearer to the latter, but close to it there is a rich capillary plexus without large vessels. A good many of the arteries enter the apical region, and break up to go, partly to the tooth pulp and partly to the periosteum, some of them reaching right from the apex to the gum; they anastomose freely with

FIG. 57 (1).



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(1) Portion of the side of the root of a tooth, the gum and alveolar dental membrane, and the edge of the bone of the alveolus.

A band of fibres is seen passing over the surface of the alveolus and dividing, some to pass upwards into the gum, others to pass more directly, across to the cementum. Numerous orifices of vessels cut across transversely are seen between the tooth and the bone.

vessels in the bone and with those of the gum, so that the blood supply is not easily interfered with.

The vascular supply of the root membrane is, according to Wedl, derived from three sources: the gums, the vessels of the bone, and the vessels destined for the pulp of the tooth, the last being the most important.

The nerve supply also is largely derived from the dental nerves running to the dental pulps; other filaments come from the inter-alveolar canals (canals in the bone, containing nerves and vessels, which are situated in the septa separating the alveoli of contiguous teeth).

It should be borne in mind that the tooth pulp and the tissue which becomes the root membrane have sprung from the same source, and were once continuous over the whole base of the pulp. A recognition of this fact makes it easier to realise how it comes about that their vascular and nervous supplies are so nearly identical.

Several observers have laid stress upon the occurrence of cells upon the surface of the cementum, deep down in the tooth sockets, which are unlike osteoblasts, but are very much like epithelial cells. It is claimed by von Brunn that the enamel organ goes far below the region where enamel is to be formed, and that it is, in fact, co-extensive with the dentine, thus necessarily intervening between the dentine and the cement-forming tissue; he describes the connective tissue bundles as growing through it to attach themselves to the dentine, and thus cutting up the remains of this enamel organ into small isolated areas, which are to be found here and there in the adult alveolo-dental periosteum.

Dr. Black describes perhaps these same cells, and believes them to be lymph cells lining lymph canals; these are always found close to cementum. He believes also, as corroborative of this view, that he has been able to trace pus infiltration along these chains of cells.

The human tooth is connected with the living organism very intimately, even though its special tissues are extravascular. For blood vessels and nerves enter the tooth pulp in abundance; the dentine is organically connected with the pulp by the dentinal fibrils; these are connected with the soft cement corpuscles, which again are brought by their processes into intimate relation with similar bodies in the highly vascular periosteum. So that between pulp inside, and periosteum outside, there is a continuous change of living plasm.

A favourable place in which to study the nature of the alveolodental membrane is the rapidly changing tooth of the crocodile; in it the membrane is very thick, its bundles of connective tissues very apparent, and down its middle portion, across which it parts when the teeth are changed, the portion nearest to the bone being more or less persistent, a row of pigment cells is to be seen.

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CHAPTER IV.

THE DEVELOPMENT OF THE TEETH.

The development of the teeth is a process which, while subject to modifications in the different groups of vertebrates, retains nevertheless in all certain essential characters, so that it becomes possible to embody its main features in a general account.

Prior to the commencement of any calcification there is always a special disposition of the soft tissues at the spot where a tooth is destined to be formed; and the name of "tooth germ" is given to those portions of the soft tissue which are thus specially arranged. All, or a part only, of the soft structures making up a tooth germ, become converted into the dental tissues by a deposition of salts of lime within their own substance, so that an actual conversion of at least some portions of the tooth germ into tooth takes place. The tooth is not secreted or excreted by the tooth germ, but an actual metamorphosis of the latter takes place. The details of this conversion can be better discussed at a later page; for the present it will suffice to say that the three principal tissues, namely, dentine, enamel, and cementum, are formed from distinct parts of the tooth germ, and that we are hence accustomed to speak of the enamel germ and the dentine germ; the existence of a special cement germ is asserted by Magitot, but as yet his descriptions await confirmation.

In the older anatomical works which the student may consult, the process of tooth development may still be found to be divided into periods, under the names of "papillary," "follicular," and "eruptive" stages.

These stages are based upon a false conception, upon theories now known to be incorrect, and may advantageously be absolutely abandoned. The account of the development of the teeth given in the following pages (based in the case of man and mammals upon the researches of Kölliker, Thiersch, Waldeyer, Röse, Leche, and others; in the case of reptiles and fishes, upon those of Huxley and Santi Sirena, and upon Hertwig's, my own, and others) will be found to differ from the older accounts published by a deservedly great authority, Professor Owen. Modern methods of research have disclosed facts heretofore not demonstrable; yet twenty years ago Professor Huxley demonstrated in a remarkable paper the incorrectness of certain of the theories then promulgated. Of the general accuracy of the following description I am, however, fully satisfied, and most of the facts may be easily verified by any one desirous of so doing.

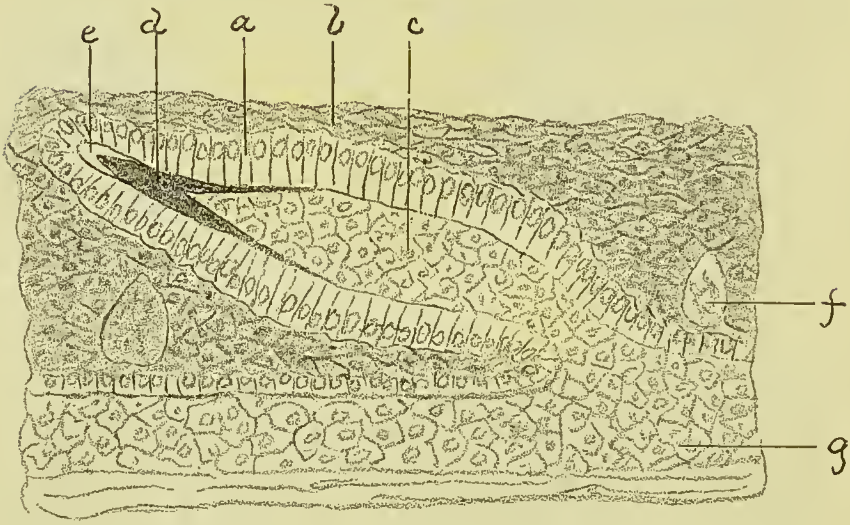
True tooth germs are generally not formed quite upon the surface, but are always situated at a little distance beneath it, in some creatures ultimately coming to lie at a considerable depth.

A few exceptions to this statement may be cited. The placoid scales of sharks, which are homologous with its teeth, are formed on the surface, as are the first teeth of Triton (newt), according to Röse, who says that they sink in subsequently. Röse also appears to regard the tooth germs of some osseous fish as in the same category, but Leche dissents from this, and, indeed, considers Röse's view as merely a question of terms.

Every known tooth germ consists in the first instance of two portions, and two only, the enamel germ and the dentine germ; and these are derived from distinct sources, the former being a special development from the epithelium of the mouth, the latter from the more deeply lying parts of the mucous membrane. Other things, such as a tooth capsule, may be subsequently and secondarily formed, but in the first instance, every tooth germ consists of an enamel germ and the dentine germ only, and the simplest tooth germs may never develop any additional parts. The existence of an enamel organ in an early stage is therefore perfectly independent of any subsequent formation of enamel by its own conversion into a calcified tissue, for I have shown that it is to be found in the germs of teeth which have no enamel; in fact, in all known tooth germs whatever.

That part of the tooth germ destined to become dentine is often called the dentine papilla, having acquired this name from its papilliform shape; and in a certain sense it is true that the enamel organ is the epithelium of the dentine papilla. Yet, although not absolutely untrue, such an expression might mislead by implying that the enamel organ is a secondary development, whereas its appearance is contemporaneous with, indeed antecedent to, that of the dentine germ. The most general account that one can give of the process is that all round the future tooth-bearing part of the jaw there is a dipping in of the epithelium, or rather of its deep layer, constituting a continuous sheet,

FIG. 58 (1).



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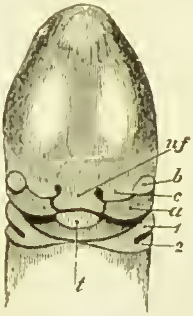
(1) Developing dermal spine of a Selachian, after Hertwig. *a.* Enamel cells. *b.* Epithelium of surface. *c.* Dentine germ. *d.* Formed dentine. *e.* Formed enamel. *f*, *g*. Cells of the mesoblast.

the tooth band or zahnleiste of German authors, which will be described in more detail hereafter.

At certain points along this a further development of the epithelium takes place, forming enamel organs, and beneath each of these a specialisation of the mesoblastic tissue goes on, forming the dentine papillæ. As the details of this process vary in different creatures I will at once pass to the description of the development of teeth in the various great groups of animals.

In Mammalia the earliest changes which will ultimately result in the formation of a tooth are traceable at a very early period: in man before ossification has set in, the lower jaw consisting solely of Meckel's cartilage, as yet not fully formed, and imbedded in embryonic tissue, and the lateral processes which become the upper maxillary bones having but just reached as far as the median process which constitutes the intermaxillary bone. That is to say, about the fortieth or forty-fifth day, in the situation corresponding to the future alveolar border, there appears in transverse sections an ingrowth of epithelium extending along the whole length of the jaw, which hardly affects the level of the surface, but is rounded on its deeper aspects. This rapidly extends more deeply into the mesoblastic tissue, so that it comes to appear in section like a tubular gland,

FIG. 59 (¹).



(¹) Embryo at end of fifth week, after Carpenter. 1, 2. First two visceral arches. *a.* Superior maxillary process. *t.* Tongue. *b.* Eye. *c.* Lateral naso-frontal process. *nf.* Naso-frontal process.

although it is really a continuous sheet or lamina of epithelium (¹), the primitive tooth band or zahnleiste of German authors.

In some animals, *e.g.*, in Ruminants, there is a considerable heaping up of epithelium over the tooth band (see Figs. 61), but Leche rightly takes exception to these figures as not representing an occurrence typical of all mammals at this early stage.

About the same time that the tooth band becomes differentiated an ingrowth of epithelium takes place all round the jaws in the situation which is to be occupied by the vestibulum oris, or groove between the lips and cheeks and the jaws and teeth, the future history of this ingrowth being that it widens and the cells which fill its interior atrophy, so as to leave an open groove.

To this ingrowth the Germans give the name of lippenfurche, a name for which no English equivalent has as yet obtained currency, and a certain amount of difference of opinion as to its exact origin exists. Röse considers that the tooth band and the lippenfurche have a common origin, and that the primitive tooth band splits longitudinally, its outer division forming the lippenfurche and its inner division being the true tooth band, whilst Baume holds that the true tooth band originates in the lippenfurche; on the other hand, Leche, an equally careful observer, considers that neither of these statements has a general applicability, and that the lippenfurche and the tooth band have a simultaneous and independent origin, at all events in many animals.

The question does not appear to me to be of any paramount importance, as, even taking Röse's own figures, the divarication of the two epithelial inflections takes place at a time when neither is advanced beyond the merest beginnings.

(¹) The epithelium having been removed by maceration or by keeping a specimen in dilute spirit, a groove would result, and this is probably what was seen and described by Goodsir as the "primitive dental groove:" but, as the student will gather from the text, there is at no time any such thing as a deep open groove like that described by him, unless it results from maceration and consequent partial destruction of the specimen.

To the heaping up of epithelium (zahnwall) (Fig. 61) over the position of the ingrowth, though it occurs in man but to a very slight extent and in only a part of the jaw, Röse attaches importance, as he considers it to be a remnant of free tooth formation in the epithelium such as occurs in the larval teeth of fishes and amphibians.

The successive stages of tooth development have been made more intelligible by the researches and models of Röse, who has made use of Born's method of modelling. A complete series of sections of uniform and known thickness are made by some form of automatic microtome and photographed or traced with a camera lucida to the same scale; every fourth or fifth section is then traced on tracing-paper, and sheets of wax being taken, the thickness of which bears a definite relation to the magnification of the sections and to the thickness and number of those represented by each sheet, the tracing-paper is laid on the wax and the wax cut out round the line of the tracing.

It is obvious that if the wax sheets are of a thickness exactly proportionate to the thickness and number of sections to which each correspond, and if the sheets so cut out are placed with their flat sides together, they will, after being united by running a hot spatula along their edges, exactly represent, on a magnified scale, the object in the solid.

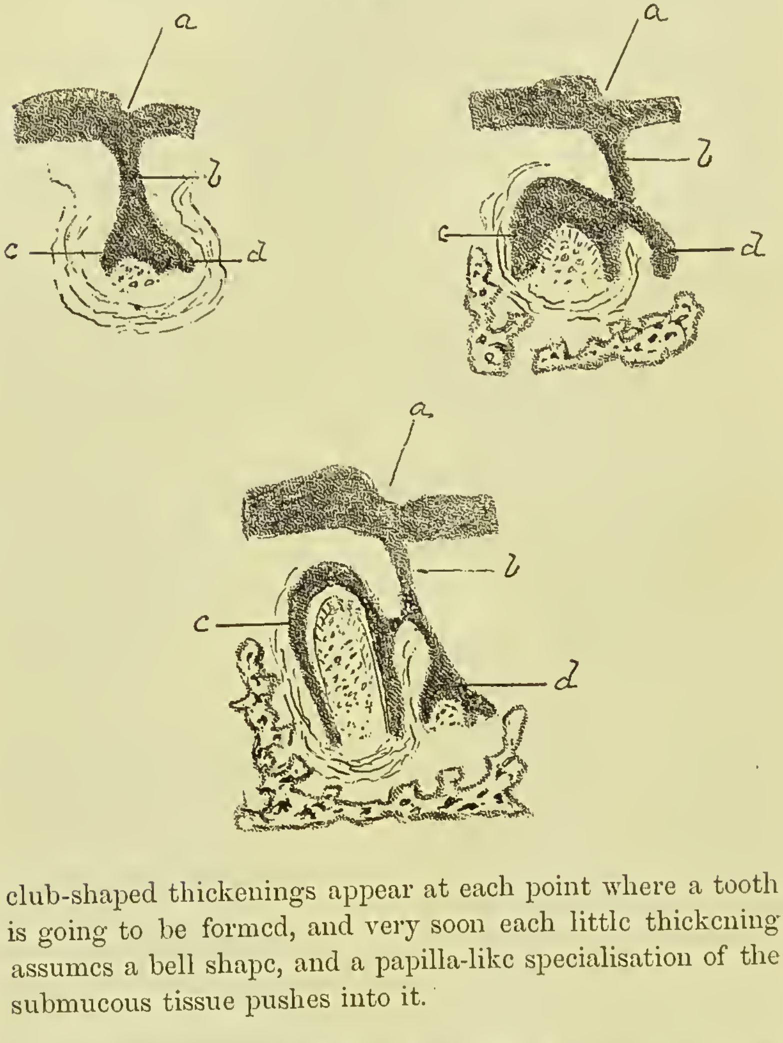
But it is of course impossible to represent thus more than one set of structures at a time, though, by making our tracing round any set that we may select, a solid model of that structure is the result.

For our present purpose the epithelial band, being the most interesting, has been specially selected by Röse.

The result of a study of these models brings into prominence the following facts. The original inflection (tooth band, epithelial lamina, or zahnleiste), at an early stage, appears to divide into two portions, according to Röse, one of which, the outer, which is nearly perpendicular, is ultimately connected with the formation of the lip furrow, whilst that with which we are more immediately concerned passes almost horizontally backwards into the tissues beneath.

This stage is reached about the forty-eighth day; then, near to, but not quite at, the free edge of the tooth band club-shaped thickenings appear at each point where a tooth is going to be formed, and very soon each little thickening assumes a bell shape, and a papilla-like specialisation of the submucous tissue pushes into it.

Fig. 60 (1).



(1) Three stages of the human tooth germ. The right-hand side of the figure is the lingual or that towards the middle line. (After Hertwig.) *a.* Primitive dental furrow. *b.* Tooth band in section. *c.* Enamel organ of first tooth. *d.* Free end of tooth band, to the inner side of which are formed the enamel organs of successional teeth.

It is to be particularly noted that this development of bell-shaped future enamel organs is not at the free end, but only very near to it, so that the margin of the tooth band is free to go on growing past them, deeper into the submucous tissue, as may be seen in the accompanying diagrams taken from Hertwig ("Lehrbuch der Entwickelungsgeschichte," 1888), and it is from this further growing part of the tooth band that the enamel organs of successional teeth, whether one or more, will be derived.

Though the formation of an enamel organ does not take place exactly at the end of the tooth band, but at one side of it, it is very near to its end. When the bell-shaped cap which is to constitute the enamel organ begins to form, it is, of course, somewhat crescentic when viewed in section. One horn of the crescent is formed almost by the terminal end of the tooth band, the other horn bends out from it a little way up, and the whole is not at all detached by any constriction from the general body of the tooth band; so that for a little time it looks as if the end of the tooth band were wholly used up in its formation; but very soon the tooth band begins to grow on beyond (Fig. 60) it, and from this further prolongation of the tooth band any successional teeth germs, if there are to be any, will be formed. But that the tooth band is not continued, to the extent shown in the first figure at all events, even when no successional tooth germ is in question, is not yet proved.

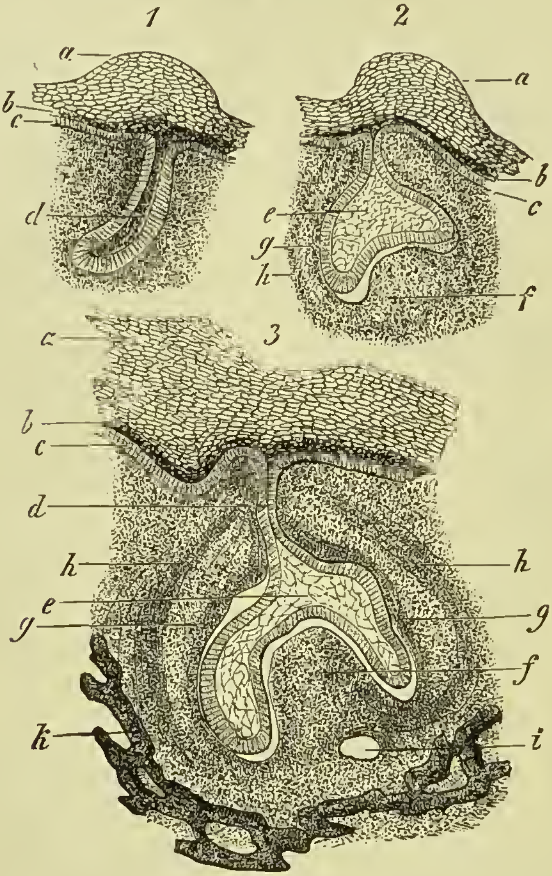
The tooth germs are formed always upon the outer or labial aspect of the tooth band, which has come to be inclined inwards towards the middle line; hence it follows that when we find that a tooth germ lies upon the lingual side of another, it necessarily belongs to a later generation of teeth, and *vice versâ*.

Some writers attach so much importance to the growth of the free edge of the tooth band beyond and to the lingual side of the forming tooth germ that they consider that wherever it exists there is a possibility, a potentiality, of a further generation of teeth being developed.

The position of the tooth germs with relation to the tooth band has been aptly compared to "swallows' nests built against a board."

While the tooth band is continuous round the whole jaw, its further development, which results in the formation of

FIG. 61 (1).



(1) Three stages in the development of a mammalian tooth germ. (After Frey.) *a.* Oral epithelium heaped up over germ (zahnwall). *b.* Younger epithelial cells. *c.* Deep layer of cells, or rete Malpighi. *d.* Inflection of epithelium for enamel germ (zahnleiste). *e.* Stellate reticulum. *f.* Dentine germ. *g.* Inner portion of future tooth sac. *h.* Outer portion of future tooth sac. *i.* Vessels cut across. *k.* Bone of jaw. These figures are not quite accurate, in that they do not show the continuation of the tooth band beyond and to the lingual side of the tooth germs, and in that the zahnwall is not a general typical structure.

tooth germs, takes place at detached points, where teeth are going to be formed. These appear about the ninth week in man.

We may now proceed to trace the further development of an individual enamel organ. The first result of rapid proliferation of cells is to bring it somewhat into the form of a Florence flask; then, as the future dentine papilla becomes more defined and pushes into it, it assumes the form of a bell with a handle, like a dinner-bell, as may be seen in the accompanying figures; and at the same time it recedes from the tooth band so that it comes to be connected with the latter only by a narrow double line of cells, as seen in section; this goes on ultimately to the detachment of the enamel organ from the tooth band.

Leche distinguishes three stages in the development of an enamel organ, which are of use in describing rudimentary organs which do not proceed to full development by giving a definite indication of the stage to which they have gone on.

1. The bud-shaped germ.
2. The bell or cap-shaped germ, without differentiation of its constituent cells.
3. The bell-shaped germ, with differentiation of its outer and inner epithelia, or complete enamel germ.

According to Leche, the detachment of the formed enamel organ from the tooth band is the necessary accompaniment of the formation of the next new successional tooth germ, and so long as the tooth band retains its connection with the surface epithelium and has a downgrowth beyond the last-formed tooth germ, so long is there a possibility of the development of more generations of teeth; so that he holds that in a region where these appearances obtain, it is a fair inference that tooth-building is not yet concluded.

In the enlargement which constitutes the young enamel organ (bud-shaped stage) the cells upon the periphery are columnar, polygonal cells occupying the central area of the enlargement. Very soon the terminal enlargement, as it grows more deeply into the jaw, alters in form; its base becomes flattened, and the borders of the base grow down more rapidly than the centre, so that its deepest portion presents a concavity looking downwards ; it might be compared to a bell, suspended from above by the thin cord of epithelium which still connects it with the epithelium of the surface, or it might in section be described as crescentic, the horns of the crescent being long, and looking downwards. Coincident with the assumption of this form by the enamel germ is the appearance of the dentine germ ; but it will facilitate the description of the process to pursue a little farther the development of the enamel organ.

A shallow furrow has by this time appeared on the free surface of the epithelium in the mouth, which corresponds with the situation of the tooth band (cf. Fig. 60), the "dental furrow." The cells on the periphery of the enamel organ remain prismatic or columnar, but those in its centre become transformed into a stellate network, in which conspicuous nuclei occupy the centre of ramified cells, the processes from which anastomose freely with those of neighbouring cells. (See Fig. 62.) This conversion of the cells into a stellate reticulum is most marked quite in the centre of the enamel organ ; near to its surfaces the processes of the cells are short and inconspicuous, and the whole process strikingly recalls the phenomena of colloid degeneration as observed in certain tumours.

The transformation of the cells occupying the centre and constituting the bulk of the enamel organ into a stellate reticulum goes on progressing from the centre outwards, but it stops short of reaching the layer of columnar cells which constitute the surface of the enamel organ, next to the dentine papilla ; a narrow layer of unaltered cells which remain between the stellate cells and the columnar enamel cells constituting the "stratum intermedium."

Mr. Leon Williams, however, does not consider that the cells have changed into a stellate form, but that this stellate appearance is an intercellular substance, from which the cells have been washed out. He states that the spaces are not empty in preparations rapidly fixed in Fleming's or Hermann's solution and examined in glycerine, but that the contents are always lost in balsam preparations. Mr. Williams is, so far as I know, the first to have observed and described the contents of these spaces; but I do not think that his observation is at all inconsistent with the view that the cells have undergone a sort of colloid degeneration, for it is characteristic of colloid changes for the nucleus to be pressed out against the periphery, and as the change goes on in a myxoma, or in colloid degeneration of a cancer, a stellate-looking tissue comes to be formed by the squeezing outwards of the nucleus and approximation of the walls of neighbouring cells, whilst the colloid material is frequently lost from the interior in cutting the section.

Mr. Eve ("Trans. Odont. Soc.," 1885) has also shown that in certain cystic tumours of the jaws the epithelium which enters into them undergoes a sort of colloid degeneration, which results in appearances almost precisely resembling the stellate tissue of the enamel organ. The cells become much enlarged, and the nuclei pressed against the cell wall; then the protoplasm of the individual cells becomes merged into a general mass, but the nuclei and, attached to them, portions of the cell walls remain, so that the resultant tissue has much the appearance of flattened cells with processes. In some places a drop of colloid substance forms within the individual cell, and the protoplasm is expanded out into a thin layer, so that the nucleus is pressed against the cell wall, thus producing the characteristic signet-ring appearance. Similar forms are to be found in enamel organs. Thus a cystic epithelium, probably identical in its origin with the enamel organs, undergoes a degenerative change, which brings it into close similarity with this part of the enamel organ.

Thus far all the cells constituting the periphery of the enamel organ are alike: they are columnar or prismatic; but from the time of the appearance of the dentine papilla those which come into relation with it become much more elongated and greatly enlarged, while those round the outer or convex surface of the enamel organ do not enlarge; indeed, according to some authors, they even commence to flatten and to atrophy at this early period. The cells which lie like a cap over the dentine germ or "papilla" as they elongate and their nuclei recede towards their extremities, take on the character to be presently described as belonging to the "enamel cells" (enamel epithelium, internal epithelium of the enamel organ).

The enamel organ, then, consists (proceeding from without inwards) of an "external epithelium," a "stellate reticulum," a "stratum intermedium," and an "internal epithelium," the external and internal epithelia being continuous at the edges or base of the enamel organ, while at its summit the external epithelium remains still, through the medium of the "neck of the enamel organ," in continuity with the cells of the tooth band, and through them with the cells of the "stratum Malpighi."

Thus the enamel organ is entirely derived from the oral epithelium, with which, by means of its "neck," it long retains a connection, so that it, and whatever products it may afterwards give rise to, are obviously to be regarded as "epithelial structures," and epiblastic in their origin. But it is the enamel organ alone which is directly derived from the epithelium; the origin of the dentine germ is quite distinct.

Degenerative changes begin to appear in the common tooth band so soon as the tooth germs are well on their way in their development, and apertures begin to form in it, so that, instead of being a flat and complete sheet, it becomes a cribriform sheet; hence a fallacious appearance of its being broken up and no longer continuous with the surface results when individual sections are viewed, it often happening that the plane of the section coincides with one of the perforations in the sheet.

But, as has already been hinted, this change does not go on uniformly everywhere in the dental lamina, but only where its work is nearly accomplished; thus at the back of the mouth, where more teeth have to be laid down, it is still a complete sheet, and to the lingual sides of the milk teeth where the successional teeth are to be formed, it also remains complete and goes on growing.

The same sort of change takes place in the necks of the enamel organs, and ultimately these, as well as the dental lamina itself, break up into isolated islands of epithelium, which sometimes seem to proliferate a little, and constitute the little lumps of epithelium known as the glands of Serres.

It is possible that these little nests of epithelium may be the site of certain new growths which sometimes arise in the jaws.

So far we have only traced the ingrowth of the epiblastic epithelium into the mesoblastic tissue beneath it, but wherever this has gone on to the formation of an enamel organ, the mesoblastic tissue seems to be stimulated to a growth which goes on to the formation of the dentine germ. Leche thinks that the darkening and crowding of the cells at first observed may be merely the mechanical effect of the vigorous ingrowth of epithelium, as he has observed it near to the end of the tooth band, *i.e.*, at points where tooth germs are not going to be formed. However that may be, in the embryonic tissue of the jaws, some little distance beneath the surface, and at a point corresponding to that ingrowth of cells and subsequent enlargement of the same which goes to form the enamel organ, appears the first trace of a dentine germ (1). This is at first a mere increase in the opacity of the part, without any visible structural change, and it occupies the concavity of the enamel organ. Thus the dentine germ appears early, indeed almost simultaneously with the formation of the definite enamel organ, but the enamel organ is far in advance of it in point of structural differentiation, and the earliest changes which result in the formation of the enamel organ are strikingly visible before a dentine germ can be discovered. Hence it has been suggested that the enamel organ governs and determines the ultimate form of the tooth. According to Dursy, the dark halo which becomes the dentine bulb is, like the inflection of epithelium which forms the enamel germ, continuous all round the jaw, while eventually it develops into prominences at the points corresponding to the enamel germs of future teeth, and atrophies in their interspaces.

From the base of the dentine bulb prolongations pass outward and slightly upwards, so that they in a measure embrace the free edge of the enamel organ, and at a somewhat later period they grow upwards till they fairly embrace the whole enamel organ.

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(1) The term "dental papilla," although eminently convenient, is associated with an erroneous feature of the older views upon tooth development; where it is employed in the following pages, the student must guard against the misconception that free papillæ at any time exist in any animal.

These prolongations of the base of the dentine bulb are the rudiments of the dental sac. In their origin, therefore, the dental sac and the dentine organ are identical, and spring from the submucous tissue: they contrast with the enamel organ, which, as before said, is derived from the oral epithelium.

To recapitulate briefly the facts which are now established beyond all question, the early mammalian tooth germ consists of three parts, one of which, the enamel organ, is derived from the epithelium of the surface; the other two, the dentine organ and the dental sac, originate in the midst of solid embryonic tissue at a distance from the surface; the one is ecderonic or epiblastic, and the other enderonic or mesoblastic.

The enamel organ is formed by a rapid increase of cells near to the bottom of a process which dips in from the stratum Malpighi of the oral epithelium; the dentine germ and the dental sac are formed in close continuity to this enamel organ from the submucous tissue.

If there were a "basement membrane" demonstrable in the mucous tissues at this early period (which there is not) the enamel organ and the dentine organ would lie upon the opposite sides of it.

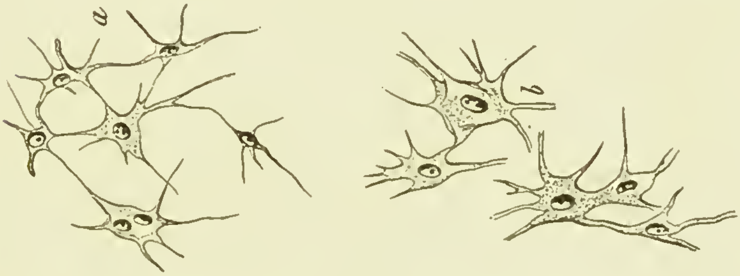
The description of the appearance of the several parts of the tooth germ has brought us to the period at which calcification first commences; but before proceeding further, it will be well to examine more minutely the structure of the several organs in which calcification takes place.

ENAMEL ORGAN.

The enamel organ, as has already been stated, forms a cap-like investment to the dentine bulb, and it is itself thickest over the apex of the latter, thinning down somewhat as it approaches the base.

It is entirely surrounded by an epithelial layer, which upon the inner surface applied to the dentine bulb consists of much elongated columnar cells, and takes the name of *internal epithelium of the enamel organ*, and upon its outer surface the name of *external epithelium of the enamel organ.* The great bulk of the early mammalian organ consists of a stellate tissue, which passes somewhat abruptly through the medium of a layer of rounded cells, the *stratum intermedium*, into the *enamel cells*, or *internal epithelium.* The essential portion of the enamel organ is this layer of "enamel cells," which by their calcification give rise to the enamel, and in lower animals, such as most if not all reptiles, the whole enamel organ is represented by little else than this layer of "enamel cells."

FIG. 62 (1).



The cells of the internal epithelium (enamel cells) form an exceedingly regular and perfect columnar epithelium, the individual cells becoming by result of their mutual apposition very symmetrical hexagons.

They are four or five times as long as they are broad, and the nucleus, which is large and oval, lies near to that end which is farthest from the dentine. It is said by Waldeyer that the sides of the cells only are invested by membrane, the protoplasm being without investment at its two ends.

Towards the base of the dentine germ, where the internal epithelium merges into the external epithelium, the cells are not so much elongated, and they there pass gradually into the cubical form of these latter cells. At their attached extremities the enamel cells are prolonged into processes which are continuous with the cells of the stratum intermedium, so that it has sometimes been concluded that the enamel cells, as they are used up in the formation of enamel, are recruited from the cells of this layer.

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(1) Cells of the stellate reticulum of the enamel organ. (From Frey's "Histology.")

The "stratum intermedium" consists of cells intermediate in character between those of the bordering epithelium and the stellate reticulum; they are branched, but less conspicuously so than the stellate cells, with which on the one hand they are continuous, on the other with the enamel cells.

The stellate cells proper are characterised by the great length of their communicating processes, and the interspace of the meshes is occupied by a fluid rich in albumen, so that the consistence of the whole is little more than that of jelly; as the structure in question constitutes the major part in bulk of mammalian enamel organs, these have been called the enamel jellies, or enamel pulps.

The function and destination of this portion of the enamel organ is not very clear: enamel can be very well formed without it, as is seen amongst reptiles and fish, and even in mammalia it disappears prior to the completion of the enamel, so that a great deal of the enamel is formed after the external and internal epithelia have come into contact. It has been supposed to have no more important function than to fill up the space subsequently taken up by the growing tooth.

It has been pointed out by Dr. Paul that this is after all not an unimportant office; the tooth sac is regular in outline, the apices of the cusps, &c., of the forming tooth very much the reverse; and it is familiar to every observer that the distribution of the stellate tissue is very unequal, even at the period of its greatest development, the forming tooth in some places coming close to the tooth sac, in others having a great thickness of stellate reticulum over it.

The external epithelium of the enamel organ is composed of cells cubical or rounded in form, and is of little interest save in that it is a matter of controversy what becomes of it. Waldeyer holds to his opinion that, after the disappearance of the enamel pulp and the stratum intermedium, it becomes applied to the enamel cells, and on the completion of the enamel is cornified and converted into Nasmyth's membrane. Kölliker and Legros and Magitot dissent from this opinion, the latter stating that the atrophy of these cells commences early, and that they actually disappear prior to the complete atrophy of the organ. The external epithelium was seen by Nasmyth, Huxley, and Guillot, but it was not very fully described until investigated by Robin and Magitot.

Recently Dr. Paul has adduced strong evidence in favour of Waldeyer's view, which has already been quoted in relation to Nasmyth's membrane.

So simple a matter as the vascularity or non-vascularity of the enamel organ is not yet settled: Wedl asserts that it contains no vessels, Magitot and Legros sharing this opinion; Xavier Sudduth has failed uniformly to detect vessels in it, but Dr. Lionel Beale, on the other hand, states that a vascular network lies in the stratum intermedium, and this is confirmed by Professor Howes and Mr. Poulton in the rat.

Dr. Paul, however, has uniformly failed to discover vessels in it, and is inclined to believe that those observers who have thought that they have detected them have been deceived by the very close resemblance to the stellate tissue of the enamel which is borne by the tissues external to the tooth sac, which, after the disappearance of the stellate reticulum and the coalescence of the external and internal epithelium, would come to lie close against the enamel cells, bringing with them their rich supply of vessels. Mr. Leon Williams believes that in some animals the stratum intermedium itself becomes transformed into papilliform elements which contain vessels, and claims that so far the enamel organ is vascular, and that his untouched photographs prove this. On the other hand, he states that this does not occur at the outset of enamel formation, and, apart from the inherent improbability of a change of an important kind in the formative organs without any corresponding change in the resultant tissue, I cannot see that the photographs exclude the explanation above given, as the stellate tissue appears always to have disappeared prior to the existence of these papillæ.

The inner surface of the enamel organ, where it is applied to the dentine bulb, presents a perfectly smooth outline, but its outer surface is thus, in some animals at all events, indented by numerous papillary projections, into which enter blood-vessels of the dental sacculus. It is believed that they exercise an influence on the formation of the enamel, to which I shall again recur; but their existence is denied by Dr. Sudduth during the period of activity of the organ.

Malassez insists much upon the significance of remnants of epithelium left after the atrophy of the enamel organ; some of these he believes that he has found in the alveolo-dentar membrane. This is confirmed, as to developing teeth, by von Brunn ("Archiv f. Mik. Anat.," Bd. xxix.), who states that in rodents the enamel organ extends far down, in fact, the whole length of the roots, and figures the fibres of the alveolo-dentar periosteum as growing through it to take hold of the cementum; it seems possible that these cells are the same which are by Dr. Black and Xavier Sudduth held to be portions of a lymphatic system.

Before leaving the subject of the enamel organ, it may be mentioned that several writers, notably von Brunn ("Archiv f. Mik. Anat.," 1887) and Ballowitz ("Arch. f. Mik. Anat.," Bd. xl.), hold that the primary function of the enamel organ is that of determining the form of the future tooth; even going so far as to suggest that its calcification with enamel in some animals is a secondary function, taken on later. In support of this contention they urge that enamel organs are universal, even where no enamel is found: and that in teeth where there is a partial investment of enamel on the ivory the enamel organ extends far beyond the enamel limits.

Moreover, they trace extensions of the enamel organ right down to the bottom of the roots in those teeth where the whole crown only is invested with enamel. Indeed, von Brunn says that it is to be traced between the roots of a three-rooted tooth, so that it may be compared to something enveloping a three-legged stool, creeping round its edges, its under-side, and finally growing down as an envelope to each leg. Its presence is confirmed by Röse, who says, that so soon as its increase downwards ceases, so does that of the dentine. Thus von Brunn holds that everywhere where dentine is to be formed there is an antecedent "form-building" investment of enamel organ; and to this, and not to any retrogression, he would attribute the enamel organ of Edentata.

But whatever may be thought as to its "form-building" functions, recent researches into aborted and rudimentary teeth of mammalia render it quite certain that in that class at all events a complete dentition of enamelled teeth was the rule, and that those which have lost, or partly lost, their teeth have arrived at this state by degeneration, so that it seems a fair inference to suppose that where enamel is absent, that also is in the nature of a degeneration.

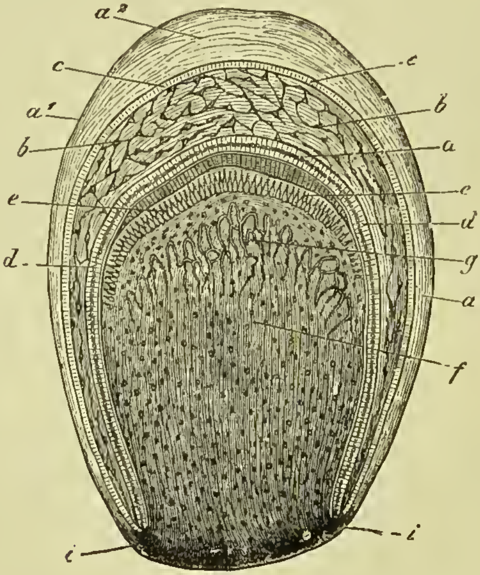
DENTINE ORGAN.

The dentine germ, or dentine bulb, of which the origin has been already described, at first was nothing more than a part of the mesoblastic myxomatous tissue of the jaw which had become more rich in vessels and cells than other neighbouring parts, but which did not present any structures essentially different from those found around it. It very speedily assumes the form of the apex of the future tooth, becoming, if it be a canine, simply conical (it has, however, been alleged that the canine papilla has at first a hint of two cusps, thereby showing its relationship to the premolars); if a tooth with two cusps, bicuspid, &c.; and coincidently with these changes the layer of cells forming its surface, which is in close relation with the enamel cells, becomes differentiated from the parts beneath it.

These cells, which are largely concerned in the formation of the dentine, form a very distinct layer, which, after the commencement of calcification, adheres more strongly to the formed cap of dentine than to the rest of the pulp, and so is often pulled away with the former when the two are separated ; hence this layer of cells has obtained the name of "membrana eboris," or membrane of the ivory ; but the student must beware of falling into the mistake of supposing that it really is a "membrane" properly so called.

Dental Follicle.—By the time that calcification is commencing, there is a tooth follicle or tissue forming a capsule-like investment around the dentine germ and enamel organ. At an early period of development the tissue forming the dentine papilla of a mammalian tooth is seen to be prolonged outwards and upwards from its base (see *h* in Fig. 61) ; these processes appear to grow rapidly upwards, so as to embrace the enamel organ ; but whether this is

Fig. 63 (1).



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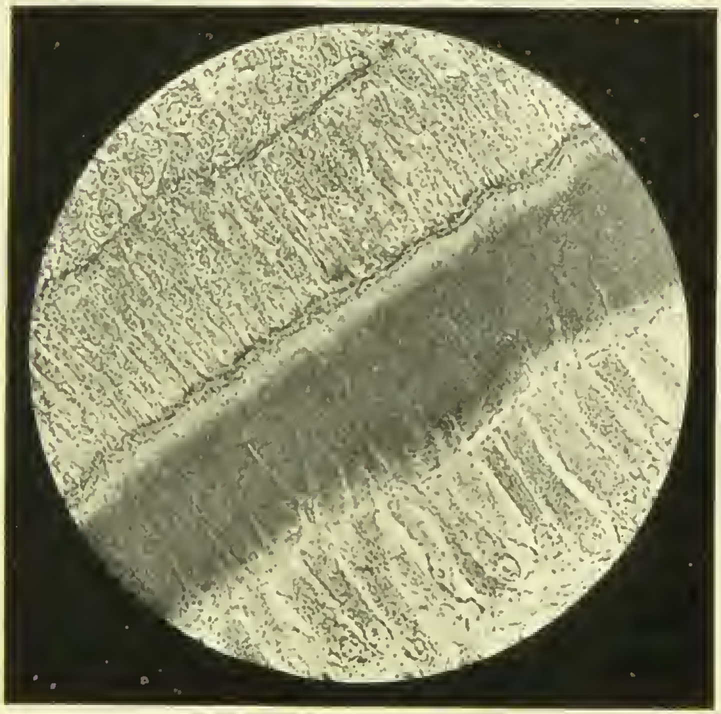
(1) Tooth sac of a calf. *a.* Tooth sac. a^1 a^2. Its outer and middle portions. *b.* Stellate cells of enamel organ. *c.* External epithelium of enamel organ. *d.* Internal epithelium of enamel organ. *e.* Odontoblasts. *f.* Dentine bulb or papilla. *g.* Vessels in dentine bulb. *i.* Points where the sac becomes fused with the base of the dentine papilla.

really so, or whether it is merely that the ill-defined tissue in which the dentine-forming organ has itself originated is in this region also becoming more pronounced, it is hard to say; probably the latter is the more true. This up-growth from the base of the dentine papilla is the first appearance of a special dental sacculus, which is thus derived from sources identical with that of the formative organ of the dentine.

Fig. 64 (1).



While these changes are going on, the tooth sac is becoming lodged in a widely open gutter of bone, which is being rapidly formed at its sides and under its base. If at this stage (see Fig. 65) the gum be stripped off the jaws,

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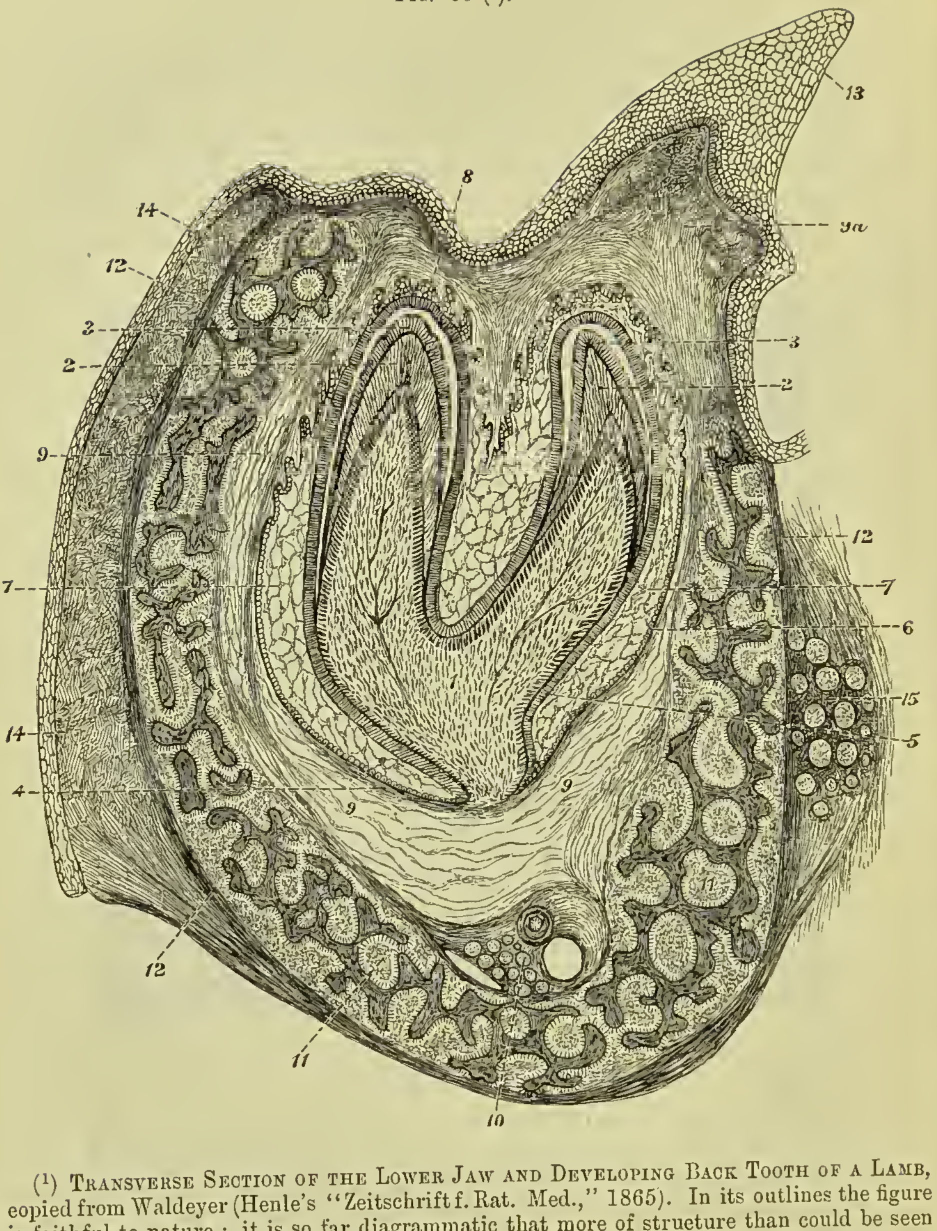
(1) General view of tissues at the time when a thin layer of dentine has been formed; from a photograph given to me by Mr. Leon Williams. At the top, to the left, is seen the stratum intermedium, next the ameloblasts, then young dentine, and below the odontoblasts, which may be seen sending processes into the young dentine.

Fig. 65 (1).



(1) Transverse Section of the Lower Jaw and Developing Back Tooth of a Lamb, copied from Waldeyer (Henle's "Zeitschrift f. Rat. Med.," 1865). In its outlines the figure is faithful to nature: it is so far diagrammatic that more of structure than could be seen with the magnifying power employed is introduced.

1. Dentine germ, with its border of odontoblasts. 2. Formed dentine. 3. Formed enamel. 4. Points where the inner epithelium and the outer epithelium of the enamel become continuous. 5. Enamel cells or internal epithelium. 6. External epithelium of enamel organ. 7. Stellate reticulum of enamel organ. 8. Papillary projections into the enamel organ. 9. Connective tissue around the sac, becoming continuous above with that of the gum (9*a*); this constitutes what is called the tooth sac. 10. Vessels and nerves of the jaw. 11. Bone of lower jaw. 12. Periosteum of the jaw. 13. Heap of epithelium over the young tooth. 14. External skin with its epidermis. 15. Muscular bundles from floor of mouth.

the developing tooth capsules are torn off with it, and are inseparable from it except by actual cutting, thus leaving the gutter of bone quite bare and empty. In fact the capsule or sac which encloses the tooth germ consists of almost the whole of the connective tissue which intervenes between the special dentine and enamel germs and the bone, which latter is originating deep in the tissues and independently of any periosteum, which is not yet differentiated.

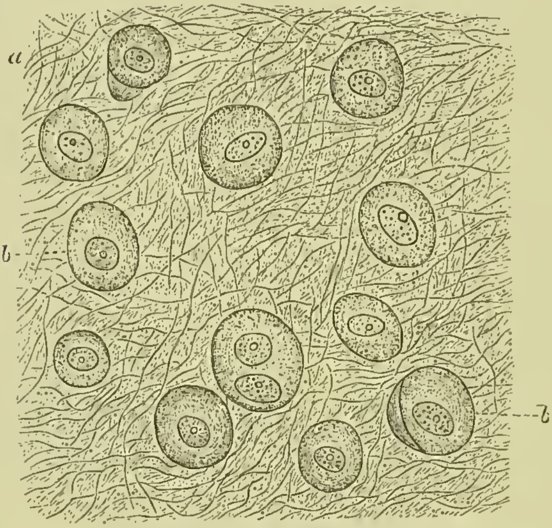
In the first instance the follicle wall is only distinguished from the connective tissue external to it by being somewhat richer in cells, vessels, and fibrillar elements ; being, in fact, more condensed or more compact. The sacs, when at their fullest development, are divisible into two layers, an outer thin firm wall, and an inner looser tissue, not very dense. At the base of the tooth sac, the follicle wall is not separable nor distinguishable from the base of the dentine papilla with which it blends. The follicle wall is richly vascular ; and over the surface of the enamel organ it is prolonged inwards in the form of villous or papilliform eminences (8 in Fig. 65), projecting into the external epithelium of the enamel organ ; to these prominences, which are analogous to the papillæ on the free surface of the gum, some authors attach much importance, as having an influence upon the direction of the enamel prisms, and so regulating the pattern formed ; but this view is by no means universally accepted. The internal or softer and looser portion of the follicle wall, which has a consistency but little firmer than that of the stellate reticulum of the enamel organ, is much developed in Ruminants, where there is to be a deposition of coronal cement. This differentiation of a portion of the dental sac is thought by Messrs. Legros, Robin, and Magitot to be sufficiently pronounced to justify its designation as a distinct "cement organ," though many later writers altogether dispute this.

THE CEMENT ORGAN.

Cementum is, according to Messrs. Legros, Robin, and Magitot, developed, just as bone is, in two distinct methods. Where it is not to be very thick, and is to clothe roots, the ossification takes place in membrane (the alveolo-dentar periosteum), but where it is to form a thick layer over the crown, as in Ruminants, a cartilaginous cement organ is formed, and we have a calcification analogous to formation of bone in cartilage.

Thus the cement organ is found in those animals only which have coronal cement, such as the Herbivora. In a calf embryo about the time that dentine calcification is commenced, there may be distinguished beneath the follicle wall and above the enamel organ a greyish layer of tissue thick enough to be distinguishable with the naked eye, and of firmer consistence than the enamel organ, from which it also differs in being richly vascular.

Fig. 66 (1).



But though it exists at this early period, it is not till later, when, after the completion of the dentine and enamel immediately beneath it, its own function is about to come into play, that it attains to its characteristic structure. This M. Magitot designates as fibro-cartilaginous, as there appear in it characteristic cartilage cells or chondroplasts, containing one, two, or rarely three cells, which have spherical or ovoid nuclei.

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(1) Cement organ of a calf. (After Magitot.) *a.* Fibroid matrix. *b* Cartilage cells and capsules.

In those creatures which have cementum upon the roots of the teeth only, no special cement organ exists, but osteoblasts which calcify into cementum are furnished by the tooth sac.

It is said that the inner layer of the tooth sac is concerned in the formation of the cement; that the outer layer, conjointly with the surrounding connective tissue, is converted into the alveolo-dentar periosteum, but I cannot myself recognise the justice of this distinction in practice. In human teeth the parts of the follicle wall or sac cease to be distinctly distinguishable at a comparatively early period, and their importance is not such as to call for very detailed description.

Another structure, once thought important, and now known to be a mere bundle of dense fibrous tissue, is the "*gubernaculum.*" The permanent tooth sacs, during their growth, have become invested by a bony shell, which is complete, save at a point near their apices, where there is a foramen. Through this foramen passes a thin fibrous cord, very conspicuous when the surrounding bone is broken away, which is called the "*gubernaculum,*" from the notions entertained by the older anatomists that it was concerned in directing or effecting the eruption of the tooth. The gubernacula of the front permanent tooth sacs perforate the alveolus and blend with the gum behind the necks of the corresponding milk teeth; those of the bicuspids unite with the periosteum of the alveoli of their deciduous predecessors.

It may perhaps assist the student, who may be perplexed in endeavouring to reconcile the statements of various authors, to give a succinct history of the views from time to time set forth.(¹)

(¹) After the present summary had been partly prepared, the author met with the very excellent *résumé* given by Messrs. Legros and Magitot, from which he has received much assistance.

Before the time of Goodsir (1838), the development of the teeth was described by Raschkow somewhat vaguely as proceeding underneath the mucous membrane; he did not, however, trace out in what precise manner the several parts of the tooth germ originated. The paper of Goodsir, giving, in the place of somewhat vague and general notions, a very definite and intelligible description of observations, was accepted without question by most anatomists, if not by all. Accordingly we find in all the text-books at and after that period, and in some even up to the present day, the description given by Goodsir reproduced almost without alteration, so that it will be worth while to briefly relate what his views were.

He believed that at an early period in fœtal life there appeared a continuous open groove, running round the whole circumference of the jaws; that from the bottom of this groove there arose isolated and uncovered papillæ, corresponding in number to the milk teeth; that these papillæ became covered in by the deepening of the groove and the meeting of its two edges over their tops, whilst at the same time transverse septa were formed, so that the several papillæ became enclosed in their own separate follicles. With the details of the process as described by him we are not concerned; it will suffice to remember that he distinguished the four stages: a primitive dental groove, a papillary stage, a follicular stage, and an eruptive stage (the latter of course at a long subsequent period).

Not only were these views accepted quite without question, but they were even extended to explain the development of the teeth in Reptiles and Fishes, and thus in the Odontographies of Professor Owen and Professor Giebel may be found accounts of the development of the teeth in reptiles and fish which are perfectly in accord with Goodsir's theory, but which, in fact, are far more inaccurate than the same theories were as applied to mammalian teeth.

Even so careful a writer as Professor Huxley, who was the first to point out that these stages really did not exist either in the frog, the mackerel, or certain other fish, accepted them without question as true of mammalia. Markusen (1) (1849) gave upon the whole a correct account of the process, referring the enamel to the oral epithelium, and Professor Huxley (1854), whilst demonstrating that the stage of free papillæ was not to be found in certain fish and reptiles (a fact also made out in the newt by Dr. Beale), clearly and strongly expressed the same view as to the origin of the enamel organ, and hence of the enamel. And whilst regretting that their hold upon the minds of anatomists has been so strong as to encourage deductions therefrom going wider and wider of the mark, I would not be understood to set small value upon the observations of Arnold and Goodsir. They were a great step in advance, and were as accurate as the methods of investigation then in use would allow of: moreover, the error in observation is very easy to account for, the epithelium having peeled off as a result of decomposition or the use of weak spirit. the state of things left does not widely differ from that described by Goodsir.

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(1) In the *résumé* given by Messrs. Legros and Magitot, before referred to, due credit is not given to the papers of Markusen and Huxley (1849, 1854) (although they are alluded to), and it appears to me that too much is given to that of Natalis Guillot (1858).

The subject rested for many years without further advances, but in 1863 Professor Kölliker demonstrated, beyond all cavil, the real origin of the enamel organ and its relations to the oral epithelium, the dentine organ, and the dental sac.

His views, substantially correct, have been elaborated by Waldeyer, Kollmann, Hertz, Legros and Magitot, Wedl, Hertwig, and others, and only in minor particulars have they been modified.

The development of the teeth of reptiles was found by a pupil of M. Kölliker, M. Sauti Sirena, to have several features in accord with that of mammalian teeth ; my own researches on the teeth of Batrachia and Fish and Reptiles, elsewhere detailed, have proved a striking general similarity in the process throughout the vertebrate kingdom.

Membrana Preformativa.—To the student of dental development, few things are more perplexing than the conflicting statements which he reads in various works as to the nature and position of the Membrana preformativa ; after having mastered with difficulty some one description of its character, he finds that many of the most recent authors altogether deny its existence. I will endeavour, therefore, so far as I am able, although not myself believing in its presence, to put the matter in a clearer light, and to point out wherein lie the discrepancies of statement.

According to the older theories of tooth development, under the thrall of which most authors have written, the tooth germ was in the first instance a free, uncovered papilla of the mucous membrane, which subsequently sank in and became encapsulated, &c. &c. (See pp. 111 and 136.) Moreover, it was taught by the older histologists that fine homogeneous "basement membranes" were to be found in a great variety of situations, amongst others beneath the epithelium of the mucous membrane, and that these were of (physiologically) much importance, inasmuch as they formed defining limits, through which structures did not pass. As a necessary consequence of these views, it was assumed as a matter of course that the "dentine papilla" must be covered over by a "basement membrane," or membrana preformativa.

Thus this membrane necessarily intervened between the enamel organ and the dentine papilla, and hence gave rise to difficulties in the understanding of the calcifying process. Henle considered that evidences of its presence speedily became lost, but that ossification proceeded in opposite directions upon the two sides of this membrane : from within outwards in the case of the enamel, from without inwards in the case of the dentine.

Professor Huxley, starting on the same hypothesis as to its position, namely, that it was between the enamel organ and the dentine papilla, came to a different conclusion as to its after fate ; relying upon the fact that a continuous sheet of tissue or membrane can be raised from the surface of the developing enamel (see p. 164), he concluded that this was the original membrana preformativa, that it afterwards became the Nasmyth's membrane, and that enamel was developed without the direct participation of the enamel organ, seeing that a membrane separated the two. My reason for doubting the correctness of these conclusions has been there given; the membrane so demonstrable is, I believe, artificial, and does not represent any naturally existing structure.

Kölliker strongly affirms the existence of the membrana preformativa, and in the older edition of his Histology held that it became converted into Nasmyth's membrane; although he now gives a different explanation of the origin of Nasmyth's membrane, I have not found a definite statement as to his recent views of the ultimate fate of the membrana preformativa.

We have thus three situations assigned to the membrane covering the dentine papilla, or membrana preformativa:—

(i.) Between the dentine and the enamel (Henle).
(ii.) Between the enamel and the enamel organ, *i.e.*, outside the enamel (Huxley).
(iii.) Between the dentine and the pulp (several writers of less authority).

We come next to those writers who deny its existence altogether, explaining on other grounds the appearances observed.

Markusen believed that it was nothing more than the part of the papilla first ossified; and Dr. Lionel Beale definitely denies the existence of a membrane in any one of the three situations above detailed, as do also Hertz, Wenzel, and Waldeyer.

Messrs. Robin and Magitot have offered a plausible explanation of the appearance of a limiting membrane over the pulp, which is briefly this: the formative pulp is rich in a clear substance of gelatinous consistency (which, in fact, forms its chief bulk), and which reminds the observer of the tissue contained in an umbilical cord. This is somewhat more dense towards the surface, where it forms a matrix for the odontoblasts and projects beyond them, so as to look, in section or at a thin edge, like a sort of varnish to the papilla. From its greater density near the surface, it may become corrugated, and so look like a folded or torn membrane. I am quite inclined to agree with the foregoing explanation.

Indeed, I think that but for the erroneous theories that the dentine germ originated as a free papilla on the surface, which would, according to the prevalent view, have been necessarily invested by a basement membrane, we should never have heard of a membrana preformativa. At all events it is difficult to imagine that such a membrane exists upon papilla formed at such a great distance from the surface as those of the snake or the lizard (Fig. 71); and if there be such a membrane, it might be a secondary development upon the surface of the mass of cells which primarily constitute the rudiment of the dentine papilla, and in that case is not a part of the general basement membrane of the oral mucous membrane; or else it must have been carried in as a sort of *cul de sac* in front of the inward-growing process of the epithelium, to which in that case it would belong rather than to the dentine germ. Neither of these suppositions commends itself as probable; and a still greater obstacle to the acceptance of a membrane in this position is afforded by the structure of Marsupial teeth (see Fig. 10), in which the membrane would be everywhere perforated by the soft contents of the dentine and enamel tubes.

It must be remembered also that basement membranes have for the most part been found to consist really of flattened cells, and to be very often incomplete and fenestrated. The latest contribution to the subject is in Mr. Leon Williams's paper upon enamel. By staining (apparently with Ehrlich Biondi stain) he has found an appearance of a distinct line of different colour at that end of the enamel cells where they approach the dentine papilla, and also at their other ends, *i.e.*, between them and the cells of the stratum intermedium. Now a difference in colour with a double stain means a difference of chemical or, perhaps, physical constitution or of reaction to a certain extent; but whether this region of difference can be rightly, on that evidence alone, described as a membrane I doubt, and Mr. Leon Williams expresses himself with some caution as to the nature of the stained lines. And Ehrlich Biondi is a very fickle stain, very slight causes apparently determining a difference. Thus the completely-formed and partly-formed dentine and enamel will often stain of different colours, and I have slides in which actually the same tissue has a different colour in different parts.

In the former editions of this book Magitot's table giving the date of appearance of the various tooth germs and the size of their calcified caps was given; but in this edition Röse's table has been adopted, the latter having shown that in all probability the age of some of Magitot's specimens was not correctly ascertained. Röse has followed His in his determinations of the age corresponding to certain lengths of fœtus, and some of the principal dates thus ascertained are as follows :—

(i.) First appearance of the dental lamina takes place from the thirty-fourth to the fortieth day.

(ii.) About the tenth week the front eight papillæ form and become imbedded in their respective enamel organs. the remaining two following in a week or so. The separating of their enamel germ from the tooth band begins about the fourteenth week.

(iii.) In the fourteenth week the tooth band extends beyond the lower milk molar, and about the seventeenth week the papilla of the first permanent molar becomes developed.

(iv.) In the sixth month after birth the beginnings of the second molar appear.

(v.) About three and a quarter years the commencement of the wisdom tooth is seen.

TABLES OF THE DATES AT WHICH THE SEVERAL STRUCTURES APPEAR IN HUMAN EMBRYOS. ADAPTED FROM RÖSE.

Length of embryo.	Age.	
12—15 m.m.	34—40 days.	First appearance of epithelial inflection. First trace of Meckel's cartilage, but as yet no trace of bone.
17 m.m.	48 days.	The inflection has (according to Röse) divided into the Lippenfurchenleiste and the zahnleiste. Deepest layer of epithelium has become cylindrical. Meckel's cartilage fully developed, and first traces of bone appear.
2·5 c.m.	9 weeks.	The zahnleiste shows alternate enlargements and depressions.
3·2 c.m.	10 weeks.	The enlargements are club-like, and the dentine papillæ are growing into them. Eight papillæ are present.
4 c.m.	11½ weeks.	In each jaw all the ten papillæ are found. The lip groove has deepened by the disappearance of the upper part of the epithelium which filled it.
11½ c.m.	14 weeks.	The milk tooth germs lie like swallows'-nests against the zahnleiste, from which they are now partly pinched off. First appearance of stellate reticulum. Behind the last milk molar the zahnleiste runs into the mesoderm, without as yet a connection above with the surface epithelium.

		MILK TEETH.												
Length.	Weeks.	I_1.	I_2.	C.	M_1.	M_2.	I_1.	I_2.	C.	Pm_1.	Pm_2.	M_1.	M_2.	M_3.
18 c.m.	17	The necks of the enamel organs of the front teeth are reduced to strings, those of the back teeth still broad; zahnleiste irregularly thickened, and in front fenestrated. The dental groove formed in front of mouth.										Dentine papillæ formed.		
24 c.m.	20	Dental groove extends to back of mouth. First trace of calcification in the incisors.										Trace of tooth sac.		

30 c.m.	24	In front of mouth much fenestration of zahnleiste. Trace of calcification in canines and milk molars.					Papillæ embraced by enamel germ.		First trace of papillæ.			Enamel germ fully developed.		
36 c.m.	29	In the milk molars there is calcification on each of cusps, but not yet united with one another.					Trace of tooth sacs.			Zahnleiste thickened.				
40 c.m.	33				Cusps united.						Trace of enamel germ.	No calcification as yet.		
		Length of Caps of Dentine and Roots.												
	9 months fœtus.	4½ m.m.	4 m.m.	2½ m.m.	2½ m.m.	3 m.m.	No calcification.					Caps on cusps.		
	Child, 4 months.	Root, ¼ m.m.	5 m.m.	4½ m.m	4—5 m.m.	3—4 m.m.						4 cusps, 1—2½ m.m.	Bud on zahnleiste.	
	6 months.	Root, 3½ m.m.	Root, 1½—2½ m.m.	Root, ½ m.m.	4—5 m.m.	3—4½ m.m.	Cap, 3 m.m.	Cap, 2½ m.m.	Cap, 1 m.m.			Caps, 2—3½ m.m.	Papillæ.	
	2 years.												4 cusps, cap, 1½—2 m.m.	
	3¼ years.	Root, 11 m.m.	Root, 11 m.m.	Root, 11 m.m.	Root, 8—9 m.m.	Root, 6—7 m.m.	Crown complete.	Cap, 7 m.m.	Cap, 8—9 m.m.	Cusps united. Caps, 5—6 m.m.	Cusps separate Caps, 1—2½ m.m.	Root, 1½ m.m.	Caps, 2 m.m.	End of zahnleiste thickened.
	5 years.													Papilla of wisdom tooth entering enamel organ.

The development of the teeth in lower vertebrates has, as already mentioned, very much that is common to them and to the higher, the principal difference lying in the arrangements for succession.

In Elasmobranch Fishes.—If a transverse section through the jaw of a dog-fish (Scyllium canicula) be examined, we shall find that the forming teeth lie upon the inside of the semi-ossified jaw-bones, the youngest being at the bottom (Fig. 67); progressing upwards, each tooth is more fully calcified till, on passing over the border of the jaw, we come to those teeth whose period of greatest usefulness is passed and which are about to be cast off in the course of that slow rotation of the whole tooth-bearing mucous membrane over the border of the jaw which is constantly going on.

In the section figured there are four teeth advanced in calcification, while beneath them are four tooth germs in earlier stages; of the former two only are fully protruded through the epithelium, the third being in part covered in; the remaining teeth are altogether beneath the surface of the epithelium, and therefore shut off from the cavity of the mouth, if the soft parts be all *in situ*.

All the teeth not fully calcified are covered in and protected by a reflexion upwards of the mucous membrane (*c* in the figure), which serves to protect them during their calcification.

But although this may be termed a fold reflected upwards, it is not, as was supposed by Professor Owen, a free flap, detached from the opposite surface on which the teeth are developing; there is no deep open fissure or pouch running round inside the jaw, as would in that case exist, and the epithelium does not pass down on the one side to the bottom of such fissure, and then ascend upon the other as a distinct layer. On the contrary, we have here that inward growing inflexion of epithelium known as the "tooth band" (zahnleiste). Although the fold is fairly easily torn away from the tooth germs which it covers in, yet in the natural condition it is attached, and there is no breach of surface; the epithelium of the jaw is well seen in the figure, in which the epithelial layer is represented as broken just at the point (between the third and fourth teeth) where the tooth band dips in.

The conditions met with in the Elasmobranch fishes are peculiarly favourable for the determination of the homologies of the several parts of the tooth germ and of the formed tooth (1). At the base of the jaw, where the youngest tooth germs are to be found, the tissue whence the dentine papillæ arise blends insensibly with that making up the substance of the thecal fold on the one hand, and, on the other, with that clothing the convexity of the jaw and giving attachment to the teeth.

No sharp line of demarcation at any time marks off the base of the dentine papilla from the tissue which surrounds it, and from which it springs up, as would be the case in mammalian or reptilian tooth germs; all that can be said is, that the dentine germs are cellular, the cells being large and rounded, while in the rest of the mucous membrane the fibrillar elements preponderate, so that it passes by imperceptible gradations into the densely fibrous gum, found on the exposed border of the jaw.

The dentine germs, and consequently the dentine, are indisputably derived from the connective tissue of the mucous membrane immediately subjacent to the epithelium, nor can it be doubted that the enamel organs are simply the modified epithelium of that same mucous membrane.

Of course there is nothing new in this conclusion, which had been already arrived at by the study of other creatures, but the sharks happen to demonstrate it with more clearness than those other animals in whom the original nature of the process is more or less masked by the introduction of further complexities.

Hence it is worth while to study carefully the relations of the epithelium constituting the enamel organs with that of the surface of the mouth. As has been already mentioned, in the normal condition of the part there is no deep fissure on the inner side of the jaw, but the epithelium passes across (from the interspace between the third and fourth teeth in the figure) on to the protecting fold of mucous membrane (*c* in fig.). The epithelium in this situation does not, then, consist simply of one layer going down on the one side and covering the tooth germs, and then reflected up at the bottom to coat the inner side of the thecal fold, but it is an inflexion of the deep layer or tooth band; it is termed "enamel organs" because over the tooth germs

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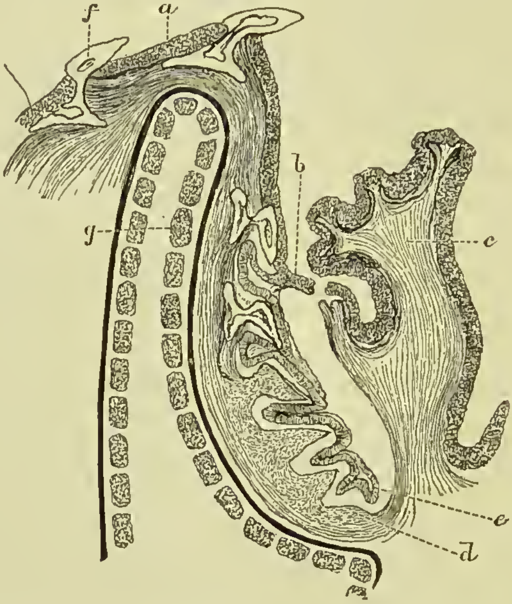
(1) Compare the description of the placoid dermal spine (p. 112).

FIG. 67 (1).



these epithelial cells assume a marked columnar character, and are very different in appearance from the epithelium elsewhere.

The terminal portion of this tooth band runs beyond the youngest enamel germ, which forms a bell-like cap over the eminence of mucous membrane connective tissue which constitutes the earliest dentine germ, and in section is of the form shown in the figure. The surface next to the dentine papilla consists of elongated columnar cells, with nuclei near to their middles, while the rest of its substance is made up of much smaller cells, some of which have inosculating processes, so that they constitute a sort of finely cellular connective tissue, very different in appearance from anything met with in mammalian enamel organs. It is sufficiently consistent to keep up the continuity of all the enamel organs, even when displaced in cutting sections, so that the whole might almost be described as forming one composite enamel organ. The columnar cells already alluded to invest the whole surface which is directed towards the forming teeth, but they atrophy somewhat in the interspaces of the tooth germs.

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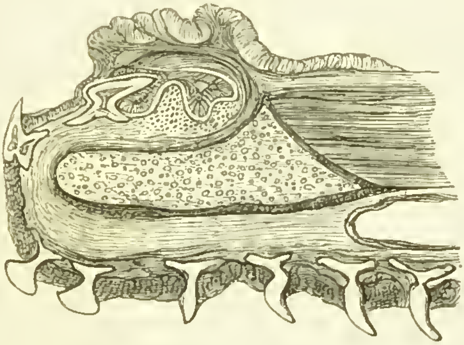
(1) Transverse section of lower jaw of a dog-fish. *a.* Oral epithelium. *b.* Oral epithelium passing on to flap. *c.* Protecting flap of mucous membrane (thecal fold). *d.* Youngest dentine pulp. *e.* Youngest enamel organ. *f.* Tooth about to be shed. *g.* Calcified crust of jaw.

FIG. 68 (1).



Before proceeding further in the description of the development of the tooth germs, it will be well to refer again to an earlier stage in the growth of the dog-fish, in which the relation subsisting between the teeth and the dermal spines is still well seen.

On the lower jaw of the young dog-fish there is no lip; hence, as is seen in the figure, the spines which clothe the skin come close to the dentigerous surface of the jaw.

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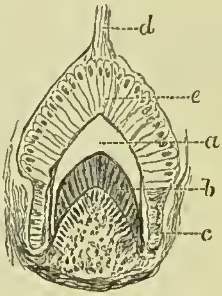
(1) Section of lower jaw of young dog-fish, showing the continuity of the dermal spines of the skin under the jaw, with the teeth which lie above and over its end.

Although there are differences in form and size, a glance at the figure will demonstrate the homological identity of the teeth and the dermal spines. As the dog-fish increases in size, this continuity of the teeth with the dermal spines on the outside of the head becomes interrupted by an extension of the skin to form a lip; this happens earlier in the upper jaw than in the lower, and at first the spines are continued over the edge and the inside of the newly-formed lip—from these situations, however, they soon disappear. In structure, the teeth and the dermal spines are, in many species, very closely similar; the latter are, however, much less often shed and reproduced, so that it is less easy to find them in all stages of their growth; I believe, however, that they follow a course essentially similar to that of the teeth.

Fig. 69 (1).



It is stated by Gegenbaur that in Selachia the mucous membrane of the mouth is clothed with spines of a structure similar to that of the teeth, and that these spines are often limited to particular regions, extending back as far as the pharynx—these same regions in Ganoids and Osseous fishes being occupied by conspicuous teeth; and Hertwig has shown that the dermal spines are developed in a manner precisely analogous to that described in the teeth, save that the germs are even less specialised.

In Teleostei or Osseous Fishes.—In passing from the consideration of the development of the tooth germs of Elasmobranch to those of Osseous fishes, the first difference to be noted is this : whereas in the former each tooth germ was, so far as the enamel germ is concerned, easily seen to be derived from the general tooth band, in the latter each enamel germ apparently often arises independently and, as it were, *de novo.* At all events, so far as my own investigations go, no obvious connection between the germs of teeth of different ages is visible ; but Heincke says that in the pike new enamel organs may be derived from older ones.

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(1) Tooth germ of an eel. *d.* Neck of enamel organ. *c.* Enamel cells. *a.* Cap of enamel. *b.* Cap of dentine. *e.* Rudimentary enamel cells opposite to that part of the dentine germ where no enamel will be formed.

This apparently independent origin of an indefinite number of teeth, having no relation to their predecessors, only occurs in the osseous fish : in them it is likely that the germs so soon become detached that their origin from any common tooth band is masked : of the development of the teeth of Ganoid fish next to nothing is known.

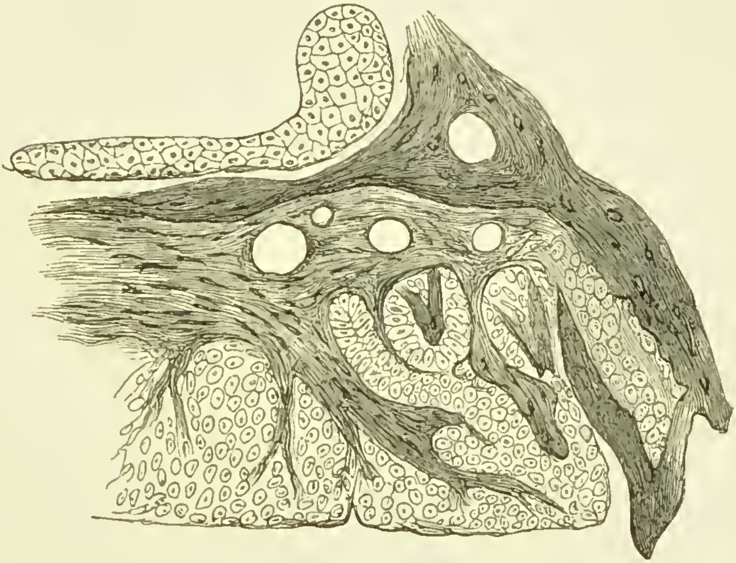
The oral epithelium, which varies much in its thickness and in other characters in different fishes, sends down a process which goes to form an enamel organ, whilst a dentine papilla in rising up to meet it comes to be invested by it as with a cap. The after-history of the process depends much on the character of tooth which is to be formed. If no enamel, or but a rudimentary coat of enamel, is to be formed, the cells of the enamel organ remain small and insignificant, as in the mackerel. If, on the other hand, a partial investment of enamel is found upon the perfected tooth, such, for instance, as the little enamel tips upon the teeth of the hake (see Fig. 37), then the after-development of the enamel organ is very instructive.

Opposite to the apex of the dentine papilla, where the enamel cap is to be, the cells of the enamel organ attain to a very considerable size, measuring about $\frac{1}{400}$ of an inch in length ; below this the investing cap of enamel organ does not cease, but it is continued in a sort of rudimentary condition. Thus, although the enamel organ invests the whole length of the dentine papilla, its cells only attain to any considerable size opposite to the point where the enamel is to be formed. The knowledge of this fact often enables an observer to say, from an inspection of the tooth germ, whether it is probable that the perfected tooth will be coated with enamel or not. In any case an enamel organ will be there, but if no enamel is to be formed, the individual cells do not attain to any considerable degree of differentiation from the epithelium elsewhere; in other words, the whole enamel organ will partake of the character of the lower portion of that represented in the figure of the tooth germ of the Eel.

Although of course there are many differences of detail arising from the very various situations in which teeth are developed in fish, so great uniformity pervades all which I have examined, that we may at once pass on to the consideration of the development of the teeth of reptiles, merely adding that it is not altogether true to say that the teeth of fish in their development exemplify transitory stages in the development of mammalian teeth.

In Reptiles, so far as the appearances presented by the individual germs go, there are few differences worthy of note to be found by which they are distinguishable from those of either fish or mammals. The enamel organ is derived from the tooth band, and the dentine organ from the submucous tissue in a very similar manner; nevertheless, there are points in the relation which the successional tooth germs bear to one another, and to the teeth already *in situ*, which are of some little interest. The constant succession of new teeth met with amongst almost all reptiles renders it easy to obtain sections showing the teeth in all stages of growth: upon the inner side of the jaw there will be found a region occupied by these forming teeth and by nothing else, which may be called "area of tooth development;" this is bounded on the one side by the bone and teeth which it carries, and on the other by a more or less sharply defined wall of fibrous connective tissue. In the Newt, for example (Fig. 70), to the left of the tooth in use are seen four tooth sacs, in serial order, the youngest being nearest to the median line of the mouth. As the sacs increase in size they appear to undergo a sort of migration towards the edge of the jaw, while simultaneously new ones are constantly being developed beyond them. In the Newt, the ingrowth of the epithelium is obviously the first step apparent; this ingrowth of a process of epithelium or tooth band always extends beyond and inside the youngest dentine papilla, and each new enamel organ is formed from its side near its growing end. New enamel organs are therefore not derived directly from the epithelium of the surface, but from the deep end of the tooth band.

Fig. 70 (1).



In the newt, the developing teeth spread out for a considerable distance towards the palate, and thus, being free from crowding, the relations of the enamel organs of three or four successional teeth of serial ages may be studied in a single section; and the arrangement so disclosed may be advantageously compared with that seen in the dog-fish. (See Fig. 67.)

The tooth sac of the newt is a good example of the simplest form of tooth germ, consisting solely of an enamel organ and a dentine germ, without any especial investment. The "germ" is wholly cellular, and on pressure breaks up, leaving nothing but cells behind it. The cells of the enamel organ are large, and resemble those of the eel; the teeth of newts have a partial enamel tip, like those of the fish referred to, but differing from them in being bifurcated, as is very early indicated by the configuration of the enamel organ.

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(1) Section of upper jaw of *Triton cristatus* (newt). To the inner side of the tooth attached to the bone are three younger tooth germs.

In the frog there is a peculiarity in the manner in which the two jaws meet, the edentulous lower jaw, which has no lip, passing altogether inside the upper jaw and its supported teeth, and so confining the area of tooth development within very narrow limits. Consequently I have been unable to satisfy myself whether the new tooth germs, or rather their enamel organs, are derived from the primitive tooth band or spring up *de novo;* analogy would indicate the former, but appearances tend towards the latter supposition.

There is a peculiarity in the development of the teeth of some reptiles in that the first formed tooth is formed, like the dermal spine of a shark, very close to the surface; in fact, Röse says that the first tooth germ of the crocodile is actually an upstanding papilla.

This, however, is not confirmed by Leche, who says he has never seen an actual free papilla, but he describes and figures in the iguana a first little rudimentary tooth almost in the surface epithelium, and shows that the tooth band sinks in deeper and deeper by the side of this, till at last the successional teeth are formed as deep as possible on the surface of the jaw-bone, into which, however, they do not sink.

In the lizards the new tooth germs are formed a very long way beneath the surface, so that the neck of the enamel organ becomes enormously elongated, for the dentine papilla is, just as in the newt, situated at first quite at the level of the floor of the area of tooth development. The teeth of the lizards have a more complete investment of enamel, hence the enamel cells are developed upon the side of the dentine germ to a much lower point than in the newt. The germs also acquire an adventitious capsule, mainly derived from the condensation of the connective tissue around them, which is pushed out of the way as they grow larger. The further progress of the tooth germ being identical with that of mammalia, its description may be for the present deferred.

Some lizards, such as Hatteria and Chamæleon, present no evidence of successional teeth being formed, though in these acrodont lizards a "tooth band" is to be seen to the inner side of the structural tooth (Röse).

In ophidian reptiles (snakes) several peculiarities are met with which are very characteristic of the order. A snake's method of swallowing its food would seem to render the renewal of its teeth frequently necessary; although I do not know of any data by which the probable durability of an individual tooth could be estimated, the large number of teeth which are developing in reserve, all destined to succeed to the same spot upon the jaws, would indicate that it is short.

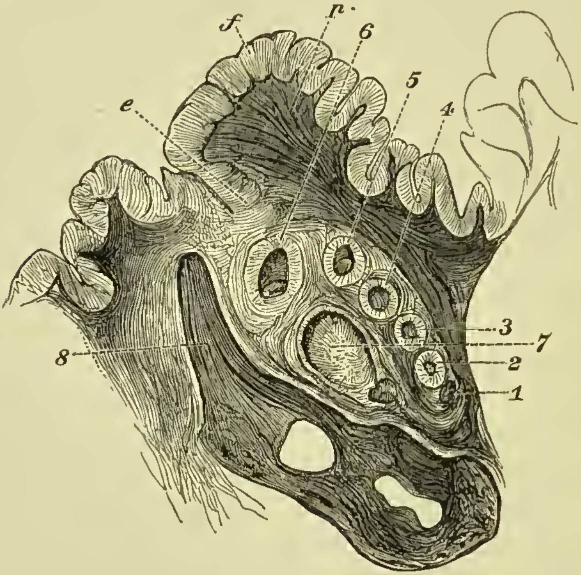
I have seen as many as seven successional teeth in a single section, and their arrangement, particularly in the lower jaw, which undergoes great displacement while food is being swallowed, is very peculiar. The numerous successional tooth sacs, instead of being spread out side by side, as in the newt, are placed almost vertically, and in a direction parallel with the surface of the jaw-bone; they are, moreover, contained in a sort of general investment of connective tissue; a species of bag to keep them from displacement during the expansion of the mouth.

The inward growing process of oral epithelium enters this case of tooth sacs at its top; and may be caught sight of here and there as its prolongations wind their way by the sides of the tooth sacs to the bottom of the area. Here the familiar process of the formation of an enamel organ and dentine papilla may be observed, in no essential point differing from that which is to be seen in other animals.

That the derivation of each enamel organ is from a part of that of the tooth band is very obvious; the dentine organs are formed in relation with the enamel germs, but apparently independently of one another.

As the tooth sacs attain considerable dimensions, a curious alteration in position takes place; instead of preserving a vertical position, they become recumbent, so that the forming tooth lies more or less parallel with the long axis of the jaw. The utility of such an arrangement is obvious: were the tooth to remain erect after it has attained to some little length, its point would probably be forced through the mucous membrane when the mouth was put upon the stretch; but while it lies nearly parallel with the jaw no such accident can occur.

FIG. 71 (1).



The tooth does not resume the upright position until it finally moves into its place upon the summit of the bone.

As has already been mentioned, there is a well-developed enamel organ with large enamel cells; from these a thin layer of enamel is formed, and thus the thin exterior layer upon the teeth of snakes is true enamel, and not, as has been usually supposed, cementum.

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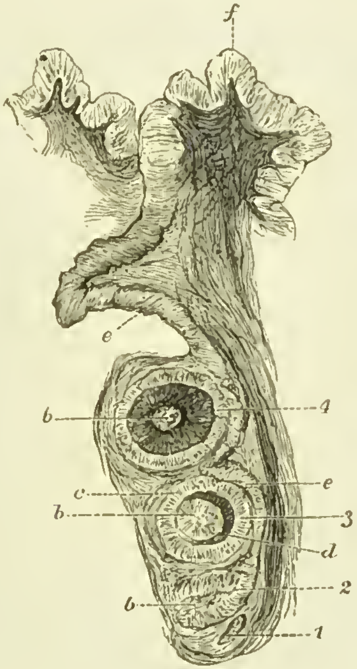
(1) Transverse section of the lower jaw of common English snake. *e.* Inward dipping process of epithelium. *f.* Oral epithelium. 1, 2, 3, &c. Tooth germs of various ages. 8. Tooth in place, cut somewhat obliquely, so that its tip apparently falls short of its surface, and does not project above the mucous membrane.

The essential feature in the development of reptilian teeth is the indefinitely repeated succession which is the typical condition, though, as already mentioned, in some instances it has become limited or entirely lost: this seems to have been the case in the most mammalian of reptiles, the Anomodont group. The question of succession has, however, of late years, become so important, and there is such a voluminous literature, that it will require special notice, and a section will be devoted to it.

FIG. 72 (¹).



(¹) Developing teeth of a snake. *f.* Oral epithelium. *e.* Neck of the enamel organs. *b.* Dentine pulp. *c.* Enamel cells. *d.* Dentine. 1, 2. Very young germs. 3, 4. Older germs.

CHAPTER V.

CALCIFICATION.

A TISSUE is said to be "calcified" when the organic structures of which it is composed are hardened and stiffened by impregnation with salts of lime. The impregnation with lime salt may go on so far that the residual organic matrix is reduced to a very small proportion, as is exemplified in the case of adult enamel, in which the organic constituents make a very minute percentage of the whole, so that practically the enamel wholly disappears under the influence of an acid; or the organic matrix may persist in sufficient quantity to retain its structural characteristics after the removal by solution in an acid of its salts, as is the case with dentine, bone, and cementum. There are two ways in which a calcified structure may be built up: the one by the deposition of the salts in the very substance of a formative organ, which thus become actually converted into the calcified structure; the other by a formative organ shedding out from its surface both the organic and inorganic constituents, and thus, so to speak, excreting the resultant tissue.

An example of the latter method is to be found in the shells of many mollusks, in which the mantle secretes the shell, and is able to repair fractures in it, without itself undergoing any apparent alteration: while the formation of dentine, bone, and enamel (1) are examples of calcification by conversion.

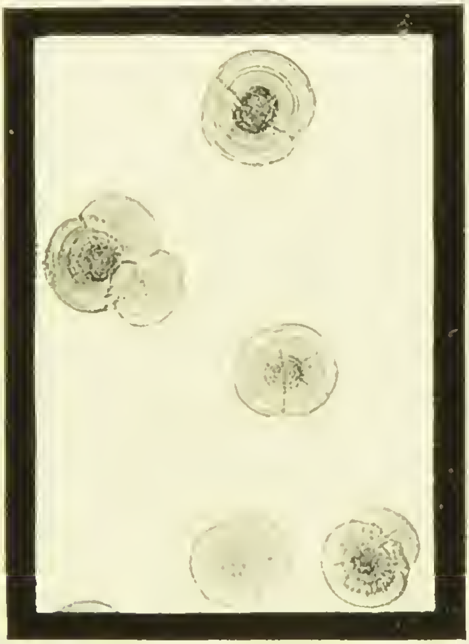
The insoluble salts of lime are altered in their behaviour by association with organic compounds, a fact which was

(1) All observers are not, however, agreed as to the formation of the enamel. (Cf. page 159.)

first pointed out by Rainie, and has been more recently worked out by Professor Harting and Dr. Ord.

If a solution of a soluble salt of lime be slowly mixed with another solution capable of precipitating the lime, the resultant lime salt will go down as an amorphous powder, or, under some circumstances, in minute crystals. But in the presence of gelatine, albumen, and many other organic compounds, the form and physical character of the lime salts are materially altered, and in the place of an amorphous powder there are found various curious but definite forms, quite unlike the character of crystals produced without the intervention of the organic substance.

FIG. 73 (1).



Mr. Rainie found that if calcium carbonate be slowly formed in a thick solution of mucilage or albumen the resultant salt is in the form of globules, laminated in structure, so that the globules may be likened to tiny onions ; these globules, when in contact, becoming agglomerated into a single laminated mass, it appearing as if the laminæ in immediate apposition blended with one another. Globular masses, at one time of mulberry-like form, lose the individuality of their constituent smaller globules, and become smoothed down into a single mass; and Mr. Rainie suggests as an explanation of the laminated structure that the smaller masses have accumulated in concentric layers which have subsequently coalesced; and in the substitution of the globular for the amorphous or crystalline form in the salt of lime when in contact with various organic substances, Mr. Rainie claimed to find the clue for the explanation of the development of shells, teeth, and bone. At this point Professor Harting took up the investigation, and found that other salts of lime would behave in a similar manner, and that by modifying the condition of the experiment very various forms (1) might be produced. But the most important addition to our knowledge made by Professor Harting lay in the very peculiar constitution of the "calcospherites," by which name he designated the globular forms seen and described by Rainie. That these are built up of concentric laminæ like an onion has already been mentioned, and Mr. Rainie was aware that albumen actually entered into the composition of the globule, since it retained its form even after the application of acid.

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(1) Calcospherites.

But calcoglobulin was also found in a comparatively amorphous condition, formed without any precipitate round a crystal of calcium chloride plunged into albumen; and it was further found that the presence of phosphates modified the result.

A precipitate obtained in gelatine and consisting of carbonate alone was at first membranous, but passed rapidly into the globular and crystalline forms: a precipitate of phosphate alone was at once crystalline without passing through any colloid stage, but a precipitate of bicarbonates and phosphates retained for an indefinite time the colloid form ; and it is noteworthy that in bone, dentine, and enamel phosphates and carbonates are invariably associated. Harting failed to produce calcospherites when experimenting with coagulated albumen, with tendons, or with decalcified bone matrix, but he succeeded with cartilage.

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(1) Thus he was successful in artificially producing "dumb-bell" crystals.

But Professor Harting has shown that the albumen left behind after the treatment of a calcospherite with acid is no longer ordinary albumen : it is profoundly modified, and has become exceedingly resistant to the action of acids, alkalies, and boiling water, and, in fact, resembles chitine, the substance of which the hard skins of insects consist, rather than any other body.

For this modified albumen he proposes the name of "calcoglobulin," as it appears that the lime is held in some sort of chemical combination, for the last traces of lime are retained very obstinately when calcoglobulin is submitted to the action of acids.

The "calcospherite," then, has a true matrix of calcoglobulin, which is capable of retaining its form and structure after the removal of the great bulk of the lime, and this stains strongly with carmine and other stains.

Now it is a very suggestive fact that in the investigation of calcification we constantly meet with structures remarkable for their indestructibility : for example, if we destroy the dentine by the action of very strong acids, or by variously contrived processes of decalcification, putrefaction, &c., there remains behind a tangled mass of tubes, the "dentinal sheaths" of Neumann, which are really the immediate walls of the dentinal tubes.

Or if bone be disintegrated by certain methods there remain behind large tubes, found to be the linings of the Haversian canals (Kölliker), and small rounded bodies recognisable as isolated lacunæ; and in the cuticula dentis we have another excellent example of this peculiarly indestructible tissue.

In point of fact, as will be better seen after the development of the dental tissue has been more fully described, on the borderland of calcification, between the completed fully calcified tissue and the formative matrix as yet not fully impregnated with lime, there very constantly exists a stratum of tissue which in its physical and chemical properties very much resembles " calcoglobulin."

It should also be noted that globular spherical forms are very constantly to be seen in the enamel cells, at the edges of the thin cap of forming dentine, and may be also traced in and around the interglobular spaces (see Fig. 27) ; moreover, isolated spherules of lime salt have been described by Messrs. Robin and Magitot as occurring abundantly in the young pulps of human teeth, as well as those in the herbivora, where their presence was noted by Henle ; perhaps all deposit of lime salts commences in this way.

In an instructive paper, Dr. Sims Woodhead (" Trans. Odont. Soc.," 1892) advocates the view that a calcification is in some measure a change in the direction of degeneration, for which there is needed (1) devitalised tissue in which we have albuminoid matter ; (2) a layer of formed material such as fibrous tissue or some membrane (in bone both of these are represented by the matrix, the fibrous tissue of which, in the centre of one of the trabeculæ, is practically deprived of cells, the layer near the surface being merely a membrane in which a few cells remained) ; (3) the layer of proliferating cells always found in the region of any foreign or dead mass, these cells being the osteoblasts of bony tissues, and amongst their functions, as regards calcification, perhaps the most important is the generation of carbonic acid.

" The osteoblasts lay down a matrix of formed material ; the more active the cells within certain limits, the greater the relative amount of the matrix. This matrix may be looked upon as inert or dead organic matter, which corresponds to a membrane through which dialysis may take place, or rather the layers near the two surfaces may be so considered, and as the molecular combinations of the phosphoric acid and lime take place about the osteoblasts (which, as before stated, during their active formative stages give off carbonic acid to render the lime for the time being insoluble), there is a continuous process by dialysis of separation of these lime salts. We look upon the formed matrix then (or dead material) as playing the part of a dialysing membrane that serves to separate the lime salts prepared in its immediate neighbourhood by the carbonic acid forming cells, &c."

If Hoppe Seyler is correct in supposing that the salt which hardens bone, dentine, and enamel is a double salt, in which one equivalent of lime carbonate is combined with three equivalents of lime phosphate, then the share taken by the carbonic acid set free becomes very intelligible. (Cf. p. 41.)

CALCIFICATION OF THE ENAMEL.

Although the calcification of the dentine commences before that of the enamel, it will be convenient to describe that of the enamel first, as being perhaps a somewhat simpler and more easily intelligible process.

Two views are held as to the formation of enamel, the one that it is formed by the actual conversion of the cells of the enamel organ into enamel, the other that it is in some sense secreted or shed out by these cells. In support of this latter theory the names of no less authorities than Professor Huxley, Kölliker, Wenzel, Magitot, and others may be adduced, but some of the grounds on which their decisions were based are appearances susceptible of a different interpretation. Kölliker considers that the cells do not undergo any direct conversion, but that the enamel is shed out from the ends of the enamel cells, the enamel fibre therefore corresponding in size and being continuous with the enamel cells whence they were shed out.

The cells would thus elaborate, and, so to speak, plaster from their free ends the material in question upon the already-formed enamel, they themselves retaining their own integrity. In support of this view may be cited the close resemblance in the resultant products in the case of enamel, and of the shells of certain mollusks, say, for example, Pinna. In the case of the mollusk the shell is formed intermittently by the margins of the mantle, which are closely applied to it, but are at any time separable, so that it is difficult to suppose that any conversion of its constituent cells can take place; but it would rather seem certain that something must be shed out from their ends, which is hardened by the deposition in or with it of lime salts. The shell of Pinna contains so large an amount of organic matter that its structure is retained even after the removal of the lime by means of an acid, and it is conceived that the cells of the mantle are at work, like so many bees plastering wax upon a honeycomb, elaborating and plastering on their products so that each one builds on to its own prism and retains for this its individuality.

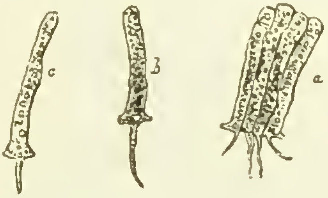
But whether the enamel cells manufacture something which they shed off their ends, or are themselves converted into hard tissue by the deposition of lime within their own substance, no one doubts that they preside over the process and determine the form of the result.

The cells of the internal epithelium of the enamel organ or enamel cells have been already in some measure described: they are elongated cells, forming a very regular columnar epithelium, and are hence rendered hexagonal by mutual apposition; they vary in their length and diameter in different animals, but always correspond in diameter with the complete enamel prisms.

To secure uniformity of nomenclature, the name ameloblast has recently been proposed for them, as being better comparable with the terms odontoblast and osteoblast.

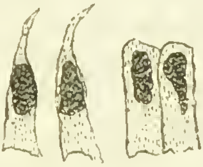
Although they are connected with the cells of the stratum intermedium by a process at their base, they often adhere more strongly to the enamel, when once this has begun to be formed, than to the rest of the enamel organ, so that when a dental sac is opened the enamel cells are most easily obtained by scraping the surface of the enamel. The cells thus torn away often have tapering processes at the ends directed towards the enamel, which were first described by my father, and go by the name of "Tomes' processes." The cells are also slightly enlarged at these extremities, especially if they have been immersed in glycerine or any such fluid which causes their shrinkage, perhaps because this end of the cell having received a partial impregnation with lime salt at its periphery, and so being rigid, is unable to contract with the rest of the cell. These enlarged, everted ends often show a very sharp contour, their trumpet-like mouths tending to confirm the statement of Waldeyer, that the protoplasm of the cell is not covered by membrane at its ends. The nucleus is large and oval, often occupying the whole width of the cell, and it lies near to that end of the cell which is farthest from the forming enamel. It contains granules, and is of delicate reticular structure; there are also generally one or several nucleoli.

FIG. 74 (¹).



Sometimes the nucleus looks squarish and angular; it is not uncommon for it to appear crescentic on section, the horns of the crescent looking towards the young enamel (Fig. 79), and there is also sometimes an appearance as though the horns of the crescent were continued into filamentous processes. If such processes have any real existence, it is very possible that these shapes of nucleus may be due to its being, so to speak, dragged upon during its recession from the forming enamel, for there is practically no doubt that the one ameloblast forms the whole length of an enamel prism, and therefore is constantly receding as more enamel is formed.

FIG. 75 (²).

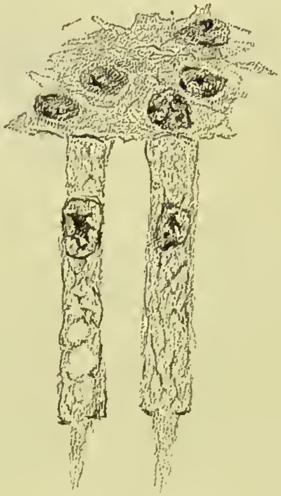


(¹) Enamel cells with Tomes' processes.

(²) Enamel cells; the two on the left have been shrunk by immersion in glycerine, and present the open trumpet-shaped ends described in the text.

There is also a delicate reticular appearance in the body of the cell, and in addition there are to be seen little spherules or oval bodies, transparent, structureless, and highly refractive, which sometimes attain to considerable size. These were first described by von Spee, and afterwards by Andrews, who believed that they represent the formative material of enamel, and attached therefore much importance to them. They stain black with osmic acid, as does also the youngest layer of forming enamel (Röse), and it has been pointed out by Leon Williams that they often, in double-stained sections, take the same colours as the contents of the blood-vessels, whence he concludes that they have some albuminous constituent. Ameloblasts vary much in length, it appearing that they are longest when enamel formation is most active, and a material thickness of enamel is to be formed. The distribution of the large enamel cells or ameloblasts coincides always with the extent to which functional enamel is going to be developed upon

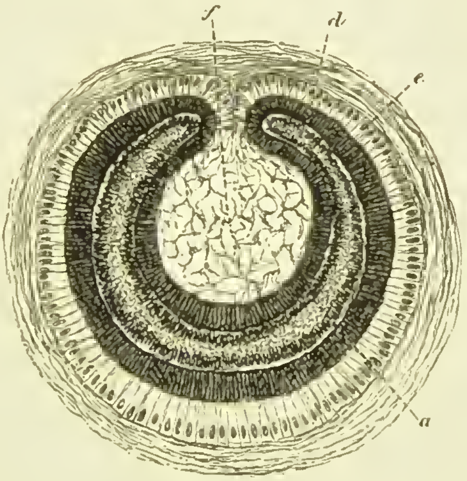
FIG. 76 (1).



Enamel cells, showing the apparently reticular structure of the plasm of the cell, the globular bodies (in the left-hand cell), and the Tomes' processes. At the top of the figure is a portion of the stratum intermedium. × 1,000.

the tooth, as shown by my own researches upon the development of the teeth of fishes. As has been already mentioned the enamel cells in some parts of the enamel organs of certain fish, such as the eel and perch, and certain Batrachia, *e.g.*, the newt, have dimensions very greatly exceeding those of the cells in the remainder of the organ. These highly-developed cells, three times as long as the corresponding cells lower down upon the dentine papilla, are in the position of the terminal cap of enamel which characterises these teeth. Moreover, in the tooth sac of the poison fang of a viper, the distribution of the large cells coincides with that of the enamel on the finished tooth.

Fig. 77 (1).



Notwithstanding all that has been written upon the subject of enamel development, the problem is so difficult that some doubt still remains as to the exact *modus operandi* of the enamel cells, though no one now doubts that they are the active agents in the process, and their diameter corresponds exactly to that of the completed enamel prism in the particular animal.

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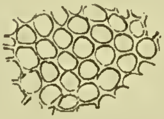
(1) Transverse section of the tooth sac of a poison fang (Viper). The crescentic pulp (*a*) is surrounded by a layer of dentine (*d*); external to this is a layer of columnar enamel cells, which, upon the exterior of the tooth, upon which a thin layer of enamel is to be formed, are large conspicuous cells. Where they pass in between the horns of the crescent, into that part which will ultimately be the poison canal, their character is lost, and their places taken by stellate cells (*f*). No enamel is formed in this latter position.

Tomes' processes are of universal occurrence in all animals which have been examined, and there is no doubt that they enter the youngest layer of enamel. And it has long been known that from the surface of growing enamel acids raise up a fenestrated membrane, as though, at this stage at all events, the interprismatic material were a little more resistant than the axes of the prisms, and it has been inferred that Tomes' processes had been pulled out of the holes thus demonstrated.

Many years ago I pointed out that in Marsupials Tomes' processes were of unusual length, and that this might have some bearing upon the question of enamel development; but from the want of material I was unable to ascertain in what way. Lately, however, I have been successful in getting material, and I believe that in marsupial enamels lies the clue to enamel development in general. The results of my investigations are more fully set out in a paper published in the "Phil. Trans.," 1897.

Fig. 78 (1).



Andrews (World's Columbian Dental Congress, Chicago, 1894) had pointed out that a fine fibrillar structure was to be seen on growing enamel, between the ameloblasts and the enamel, and these fibres have been seen and figured also by Leon Williams; but neither of these observers have appreciated their full importance, owing to their having only investigated enamels in which their existence is very transitory. But in the tubular enamel of marsupials they persist, and can be seen extending the whole distance between the ameloblasts and the layer of young dentine, and can hence be studied to far greater advantage. They are there clearly seen to be merely very long Tomes' processes (which are in fact fibrils broken off short), and they can be clearly seen to be prolongations of the plasm of the ameloblasts, which, as rightly described by Waldeyer, have no membrane across their free ends; their behaviour to stains is the same as that of the cell contents. Although it is convenient to speak of them as fibrils, they do not show any minute fibrillar structure; where they leave the parent cells they are apparently not much, if at all, smaller than these cells,

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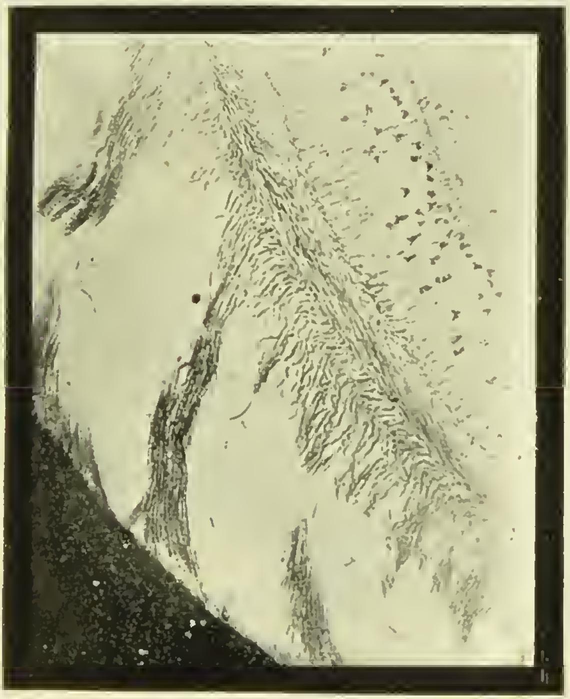
(1) Fenestrated membrane raised from the surface of forming enamel by dilute hydrochloric acid.

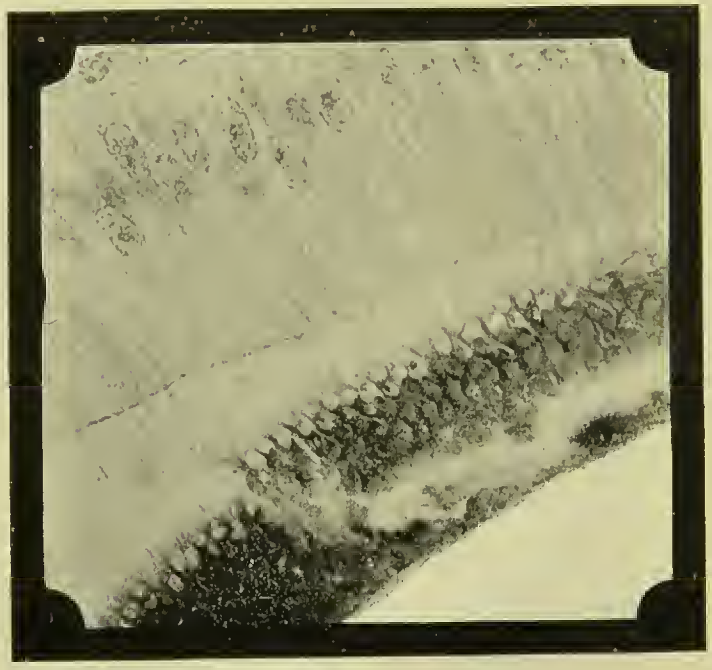
FIG. 79 (¹).



(¹) From a developing tooth of Macropus. At the right-hand top corner is the stratum intermedium, next the ameloblasts, with somewhat angular nuclei; and from these soft fibrils extend in places right across to the dentine, which is the dark mass at left bottom corner of the figure. A short distance from the ends of the ameloblasts the fibrils are seen to change their direction abruptly. From "Phil. Trans.," 1897.

the apparently small size of Tomes' processes being due to their having been drawn down by being pulled from the enamel. They are soft and extensile, so that they may be drawn down to a mere thread before they break (see Fig. 80), and their direction exactly coincides with that of completed enamel prisms, running straight where these do so, and taking abrupt bends when these bend, as they often do, almost at right angles in certain parts of a kangaroo's enamel.

FIG. 80 (1).



In decalcified sections of developing marsupial enamel, if, as generally happens, they are in the least degree oblique to the axes of the prisms, there is a most conspicuous appearance of a sort of honeycomb, the septa of which take stains strongly. The Tomes' processes, and their continuations the fibrils, enter the spaces of this honeycomb, and in favourable sections which happen to be transverse to the honeycomb are seen to fill the holes. This conspicuous honeycomb is exactly the same thing as the fenestrated membrane already alluded to (p. 164) in human and other mammalian enamels, but in enamels which are to have solid prisms it occupies only a very small vertical depth, while in tubular enamels it is of material thickness ; since investigating it in marsupials I have seen it in the pig and the sheep quite recognisable as a honeycomb, and it is distinctly visible in some of Mr. Leon Williams' photographs. But although it is comparatively thick in marsupials, yet it is in them, like the

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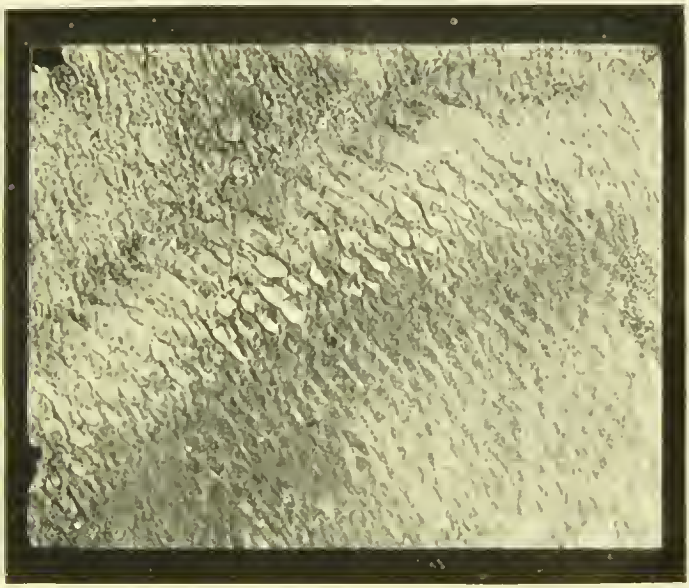
(1) Halmaturus. Ameloblasts, Tomes' processes, and youngest part of enamel, which is cut slightly obliquely, and has the appearance of a honeycomb. The Tomes' processes are drawn out thin by the slight displacement of the ameloblasts, especially at the left of the figure, and their continuations may in places be seen in the openings of the honeycomb. × 1,000. From "Phil. Trans.," 1897.

Fig. 81 (1).



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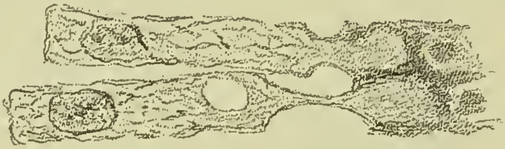
(1) Halmaturus. The ameloblasts, cut so obliquely as to be hardly recognisable in the figure, lie to the left upper side of the figure ; next comes the honeycomb region ; while the lower part of the figure is occupied by more advanced enamel, in which the fibrils may be seen, cut obliquely, as darker masses. Thus in the earliest honeycomb stage the septa stain more strongly than their contents, but at a later stage the fibrils stain more deeply than the septa. × 1,000.

fenestrated membrane of older observers, a transitional structure belonging to one—the earliest—stage of enamel calcification, and when a little farther advanced in calcification it loses its resistant power and becomes dissolved by the decalcifying agent. Hence in decalcified sections the fibres are seen at first, close to the ameloblasts, free; then attached together by the honeycomb; while deeper in the forming enamel they are more or less free again.

The exact relationship of the fibrils to the cells of the honeycomb was at first difficult to understand, for while in cross section they are seen to occupy the lumen of each cell, and could be traced in this position in longtitudinal sections also, yet, especially when drawn out so as to be thinned, they seem to be adherent to the septa. Moreover, the septa of the honeycomb are thicker than the amount of interstitial substance found between the prisms in complete enamel would account for. But I presently found that although their external portions ran continuously into the substance of the septa, their internal portions were still soft, so that the fibril slightly drawn out took on a sort of hour-glass shape, its ends attached to the ameloblasts and to the septa of the honeycomb remaining of their original diameter, while the intervening portion was drawn out into a thread. Hence it appears that the first changes in the fibril towards calcification take place in its exterior, and progress towards its interior, which in the case of marsupial tubular enamel they never reach, the prism continuing to have a canal with soft contents down its axis. But in enamels with solid prisms the full calcification of the

FIG. 82 (1).



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(1) Halmaturus. Ameloblasts showing their relation to Tomes' processes and to the honeycomb; the latter is cut slightly obliquely, so that to the right a second cell is opened into.

whole thickness of the fibril follows very close upon the heels of the first honeycomb change, and so the nature of the process is masked.

It is undesirable in an elementary text book to enter at length into the reasons which have led me to my conclusions —they may be found in the paper referred to—but they are :—

That the ameloblast itself does not calcify.

That each ameloblast furnishes a fibrillar process, continuous with its own plasm, which serves for the entire length of an enamel prism.

That calcification and the changes preparatory to calcification take place in or round each fibril, quickly reaching its central axis in solid prism enamels, but never reaching it in tubular enamels.

It will be seen that the appearances are consistent either with the calcification of the fibril, or with calcification going on round it, and, so to speak, squeezing it down to smaller dimensions or obliterating it.

The exceedingly small amount of organic matter present in completed solid enamel might seem to point to the latter being the preferable view, but were this so, one might have expected the individuality of the prisms to be lost, whereas there is an appreciable amount of interstitial substance demonstrable between the prisms.

It has been pointed out by Mr. Leon Williams that the axis of the ameloblasts seldom coincides with that of the prisms : this is the case, the ameloblasts always standing nearly at right angles to the dentine surface. But though these fibrillar prolongations start off in this same direction, they, in many cases, change their direction quite abruptly a little way from the cell, and the directions which they assume do correspond exactly with those of the prisms in the finished enamel. The identity of the fibrils with the ultimate canals of marsupial enamel is further shown by the fibrils being, in the more advanced parts of the enamel, spiral.

If my theory of enamel formation be correct, it serves to explain much that was heretofore perplexing; in the first place in marsupials, the extent to which the tube system exists varies much in different members of the group, and even in those in which it is most rich, the tubes become smaller as they approach the outer surface and die out well before they reach it; so that it is quite obvious that the same enamel organ is capable of forming both tubular and solid enamel, and there can hardly be any very fundamental difference in the processes.

Again, the enamel organ of a marsupial, prior to the formation of any enamel, is absolutely indistinguishable from that of another mammal; and tubular enamel reappears sporadically amongst other very diverse mammals, for instance in the Hyrax, in certain Insectivora, in the Jerboa among rodents, and, as an abnormality, occasionally in the first formed portions of human enamel.

But if tubularity is a stage through which every enamel prism passes, the difficulty of accounting for animals whose allies have all lost it, re-acquiring or developing it, disappears. And although the examination of human or other solid developing enamels might never have led me to this interpretation, yet a re-examination of them after having arrived at it convinces me that it is equally true of all.

In like manner the tubular enamels possessed by fish, which in some instances contain tubes entering from the dentine, in others from the free surface, and yet in others from both sides, at once become more explicable, but the development of these enamels requires to be fully worked out before much can be said about them.

Andrews unquestionably had the fibrils of the ameloblasts under observation, and was, so far as I know, the first to describe them. But he described them as coming from the cells of the stratum intermedium, which they certainly do not; and he speaks of them as a fibre network, which, when the enamel rod is fully calcified, is wholly obscured; and neither he nor Leon Williams appreciated the importance of their rôle nor their relations to the prism; indeed, I doubt if it was discoverable elsewhere than in a tubular enamel. The latter observer noticed the complexity of the course of the fibres which he saw, but apparently did not connect it with the complexity of the course of the enamel prisms in the animals from which his sections came. But in a much earlier paper ("Dental Cosmos," 1884) he came very near to my present views when he wrote: "As the formation of the enamel progresses, these cells recede, leaving within the formed enamel what appears to be a fibre of living matter in the centre of the enamel prism."

Röse comes very near to my views and correctly figures the appearances so far as they are visible in human enamel. He, however, takes a somewhat different view of the process; he describes the young enamel as like a honeycomb, with Tomes' processes in the cells of the honeycomb. He considers that young enamel, like young dentine, has an organic matrix fairly rich in lime salts, but as yet not by any means fully calcified, and that the lime salts are first deposited fully in the Tomes' processes, so that at a certain stage young enamel consists of thin prisms (calcification in Tomes' processes) with a large amount of interprismatic substance; the prisms then thicken, so that finally there is a mere trace of cement substance between them.

Von Spee and Andrews consider that the globular bodies described by them in the ameloblasts, and particularly near their free ends, coalesce and merge into the enamel substance, the fibres he describes perhaps serving as a sort of scaffolding to determine their arrangement. This again is not far from hitting the true nature of the process, and this idea is adopted, with modifications, by Leon Williams, who, in his later paper ("Dental Cosmos," 1896), holds that these globular bodies pass out from the ameloblasts, and are seen to be connected with one another by plasm strings, several to each prism, which strings can be seen in the body of the ameloblast, where they constitute the reticulum above described. He holds that in the formed enamel rod these globular bodies are more or less compressed into disk-like shapes, and are sometimes nearly, or quite, melted into one another. This is in effect very much going back to the view of Harting, who wrote: "Les prismes, qui composent l'émail des mammifères, ne sont évidemment que des piles de calcospherites très petites," &c.

Leon Williams further says, "Around the skeleton thus formed, which constitutes the real structure of enamel, the albumen-like substance flows, supplying the cement substance, and probably the mineral matter for the whole."

This view differs from that propounded in the text, in that it does not recognise the preponderant importance of the ameloblast processes, and in that it puts first the formation of the prisms, to be afterwards run together by a cement substance, whereas my preparations show, I think, beyond dispute, that the first thing formed is the periphery of the prism and the uniting cement substance, for in the honeycomb the septa of contiguous cells are already united and appear homogeneous, which is a sequence of events quite different from that which he indicates.

Kölliker, partly upon the ground that ameloblasts can be seen of the same size and form at all stages of enamel formation, held that enamel formation was one of secretion, the enamel being shed out, so to speak, from the free end of each enamel cell; hence the prisms of the enamel will correspond in size and number with the cells of the enamel epithelium; the processes of the enamel cells he regards as being fragments of this hardened secretion which are still clinging to the parent cell.

M. Magitot ("Journal de l'Anatomie de M. Ch. Robin," 1879) revived this view, describing each cell as terminated, towards the forming enamel, by a little plate of dense material through which by some process of exosmosis the constituents of enamel travel out. He notes that these plates often cohere so as to form a sheet, but says nothing of their being perforated. No one, however, who had seen the enamel cell of a marsupial with the tapering process five or six times as long as itself which had been pulled out of the young enamel would be satisfied with the excretion theory as so expressed.

Schwann believed that the enamel cell was constantly increasing at its free end (*i.e.*, that next to the enamel), and that the new growth, or youngest part of the cell, is calcified as fast as it is formed; this view differs little from that of Kölliker, who prefers to express it by saying that this end of the cell is constantly shedding off or secreting a material which becomes external to itself. My father, Waldeyer, Hertz, and many others, believed that the cell growth takes place not at this free end, but at the attached nucleated end, and that it is the oldest portion of the cell itself which receives an impregnation with salts and forms the enamel.

Upon the question of the nature of the globular appearances and smaller beads observed in the ameloblasts, I do not yet feel in a position to offer any positive opinion. It may be that von Spee, Andrews, and Williams are right in supposing it to be material elaborated for the purpose of calcification, and they may be right in supposing that these masses migrate bodily from the ends of the cells; but I do not consider the evidence to be conclusive. However, there is no doubt that they are there, and they are not a usual sort of cell contents.

Mr. Leon Williams describes appearances which lead him to believe that there is a membrane at both ends of the ameloblast, because in some double-stained preparations there is a sharply defined line of a different colour, both between the enamel and the dentine at the earliest period of calcification, and at all periods between the ameloblasts and the stratum intermedium. But differences in staining occur frequently in the very same tissue, and merely indicate a slight difference in state, and I am perfectly certain that there is no membrane over the free end of the ameloblast after the formation of its fibrillar prolongation; whilst in intervals between two fibrils there is often a very defined line, which, if the section does not happen to lie exactly along the central axis of the cell and its process, looks to be continuous over many cells and their processes, so that the appearances are open to a different interpretation. Mr. Williams himself is aware that there is no membrane and can be no membrane later on; and appearances of membranes seen in section are open to so many fallacies that, where there is an *à priori* improbability in the existence of one in a particular position, it is safer to doubt its existence until it has been demonstrated as a sheet.

With regard to the other constituents of the enamel organ there is not very much to be said; behind the ameloblasts come the large round cells of the stratum intermedium, to which it has been customary to attribute the function of recruiting the enamel cells, with which some observers have believed them to be connected by processes. After the disappearance of the stellate reticulum, the tooth sac, rich in blood-vessels, shrinks down upon the stratum intermedium; and hence has arisen the mistake of supposing that the enamel organ contains blood-vessels, the strong resemblance of the structures just outside to the stellate reticulum lending itself to this mistake. So far no observer has satisfactorily shown that any vessels enter the enamel organ proper. Since, then, this layer is made up of large cells and intervenes between the ameloblasts and their blood supply, it is highly probable that it takes some active share in the elaboration of the materials required for enamel formation, but what that share is is unknown. The inner surface of the tooth sac is frequently produced inwards into papilliform eminences, to which some observers have even attributed the function of planning the pattern of the enamel prisms, and when it has shrunk down upon the stratum intermedium, these are said in some cases to become even more conspicuous.

Mr. Leon Williams, seeing this large development of the cells of the stratum intermedium distributed over vascular papilliform shapes, has attributed to the cells a glandular function, and sets down to them a very large share in enamel formation in the way of elaborating products for calcification. But I think this is hardly a safe inference ; in the first place this particular structure does not arise till after some enamel is already formed, and there is no known difference between the enamel formed before and after its development ; moreover, it is only in some animals that it is at all well marked, and their enamel is not different in any known way from those that have it not. Upon the whole, then, we must admit that although a good deal of advance has been made towards a clearer conception of the process, there still remains a great deal to clear up in enamel formation. The ultimate fate of the external epithelium has been already treated of under the head of Nasmyth's membrane, so no more need be said here.

Calcification of the Dentine.—The dentine is formed upon the surface of the dentine bulb, or papilla, from without inwards, so that no portion of dentine once calcified can receive any increase in external dimensions ; all additions must take place upon the interior of the dentine cap. The nature of the dentine bulb has already been to some extent described ; it remains to consider somewhat more minutely the nature of its surface. The cells constituting the membrana eboris, to which Waldeyer has given the convenient name of " odontoblasts," form an exceedingly sharply defined layer upon the surface of the dentine wall, being arranged in a single row ; the cells immediately beneath them differ strongly from them, so that there is not so marked an appearance of transitional structure as may be seen in the stratum intermedium of the enamel organ. Nothing whatever like the linear succession of formative cells, which, by coalescence at their ends went to form the dentinal tubes, as described by the older writers, is to be seen.

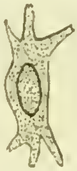
The odontoblast cells vary in form according as the dentine formation is actively going on or not, but at the period of their greatest activity they are broad at the end directed towards the dentine cap, so as to look almost abruptly truncated. The several processes of the cells have already been described ; there are, however, sometimes several "dentinal processes" proceeding from a single cell, and Boll has counted no less than six.

The cells are finely granular, and are, according to Waldeyer and Boll, destitute of all membrane ; the nucleus is oval, lies in that extremity of the cell which is farthest from the dentine, and is sometimes prolonged towards the dentinal process so as to be ovoid or almost pointed.

The dentinal process passes into the tubes of the dentine, and it frequently happens that, when the membrana eboris is only slightly separated from the dentine, these processes, which constitute the dentinal fibrils, may be seen stretching across the interval in great numbers.

The odontoblasts, as may be seen from Fig. 64, are fitted rather closely together, and there is not very much room for any other tissue between them, so long as the formation of dentine is actively going on. Prior to its commencement, however, the cells are not so square at their ends, and the appearance of the thin edge of such a pulp suggests the idea that they are bedded in a transparent and structureless jelly, which projects a little beyond them. To render my meaning more clear by a homely illustration, the surface of the pulp at this stage reminds one of the clear jellies put upon the table with strawberries or the like buried in them, near to, but beneath the surface.

Fig. 83 (1).



When the pulp has completed, for the time being at all events, the formation of the dentine, the odontoblast cells become more elongated and more rounded in their outline and taper off towards and into the dentinal process, instead of having truncated ends.

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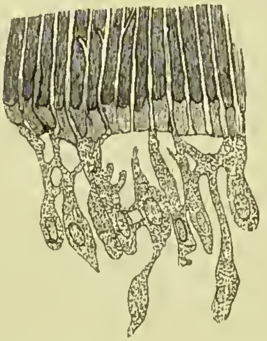
(1) Isolated odontoblast cell.

The cells figured by Lent as the formative cells of dentine, I regard as odontoblasts taken from an adult tooth, the period of formative activity being past, and I am inclined to think that his views on the subject of development are open to criticism, as being based upon the appearances presented by such old cells.

Several more or less divergent views as to the exact method of development of the dentine have from time to time held the field, the question turning mainly upon the part played by the odontoblasts. The close relation of these cells to the dentine, their change in form according as dentine building was or was not actively going on, their resemblance in position and apparent consistence to osteoblasts, and the absence of any other of the large cells which we associate elsewhere with elaboration of special products, would naturally lead to the inference that they were the chief factors in the segregation of lime salts and their incorporation in the dentine, a view which has obtained many adherents.

Fig. 84 (1).



According to this view, which is supported by Waldeyer, Frey, Boll, Dr. Lionel Beale, and many other writers, the dentinal fibrils, the dentinal sheaths, and the matrix between these latter, are alike derived from the metamorphosis of the odontoblast cell. In other words, the three structures in question may be taken as being three stages in the conversion of one and the same substance: thus we have the dentinal fibril in its soft condition, little more than the unaltered protoplasm of the cell, then the dentinal sheath, one of those peculiarly resistant substances which lie on the borders of calcification; and lastly, the matrix, the completed, wholly calcified tissue.

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(1) Odontoblasts *in situ*. After Waldeyer.

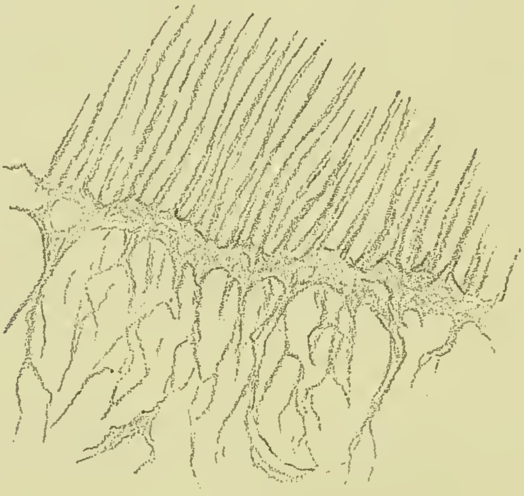
In other words, it has been supposed that the most external portions of the odontoblasts undergo a metamorphosis into a gelatigenous matrix, which is the seat of calcification, while their most central portions remain soft and unaltered as the fibrils. Intermediate between the central permanently soft fibril and the general calcified matrix is that portion which immediately surrounds the fibril, namely, the dentinal sheath; as expressed by Dr. Lionel Beale they are protoplasm, formed material, and calcified formed material.

This view differs but little from that of von Ebner and Röse, which, however, is to some extent intermediate between the older theory and that advocated by Mr. Mummery; they believe that the whole of the dentine is derived from the odontoblasts, but that while their axial portions persist as dentinal fibril, their peripheral portions become metamorphosed into a delicate fibrillar gelatigenous tissue, a connective tissue in fact, which, forming the matrix, receives an impregnation with lime salts.

It will be remembered that von Ebner has shown the existence of a delicate fibrillar structure both in bone and in dentine; and his investigations have been carried further by Mr. Mummery, whose view, briefly expressed, is that the dentine matrix is due to a calcification in a delicate connective tissue which has not been derived from the odontoblasts at all, but from the general connective tissue of the pulp. He confirmed von Ebner's observation that in the completed matrix now and again traces of a much masked fibrillar structure were to be found, especially in teeth which had undergone the slow decalcification attendant upon the early stages of dental caries. But he further showed that by the use of Koch's method as modified by Weil a connective tissue was to be demonstrated in the periphery of the pulp, which connective tissue apparently ran continuously into the matrix, somewhat as Sharpey's fibres run into bone.

According to him, dentine is developed very much like a membrane-bone, there being, however, this difference: that in the case of dentine long protoplasmic processes from each odontoblast cell persist, though the cells themselves do not become enclosed in the forming tissue; in the case of bone, some at least of the osteoblasts do become boxed in, and persist as the branched cells which occupy the lacunæ. He has traced these connective tissue bands passing between the odontoblasts and running into the dentine, while, on the other hand, their continuity with the general connective tissue of the pulp is easily demonstrable. They are, however, not well seen in sections which run exactly in the plane of the length of the odontoblasts, which in that case

FIG. 85 (1).



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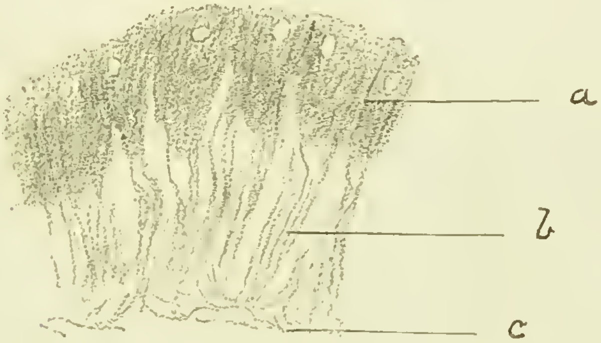
(1) At the top of the figure is seen the formed dentine; next comes a layer of forming dentine, to which a number of connective tissue bundles adhere. (After Mummery.)

are apt to obscure these very delicate fibrils somewhat; and there appear to be cells applied to these bundles of connective tissue which are distinct from the odontoblasts, and recall the cells upon the osteogenetic fibres of bone.

For the details of the reasons which have led him to adopt this view, the reader must refer to his original paper; but a very strong argument in its favour is derived from a study of the development of vascular dentines.

In some papers in which I described these dentines, I made mention of a very distinct layer of straight parallel fibres which abut upon the forming dentine, and which I at that time regarded as peculiar large, or rather long, odontoblasts. But on going over my old preparations with Mr. Mummery, and studying those which he had prepared, I soon became convinced that I had been in error in so regarding them, and that they really are a layer of specially arranged connective tissue fibres. For they are devoid of any nuclei, and quite lack the, so to speak, succulent appearance of true odontoblasts.

Fig. 86 (¹).



Though they so far resemble them as to pull away in a continuous sheet adherent to the dentine, and of perfectly uniform thickness, yet in suitable preparations they can be seen to be continuous with the connective tissue framework

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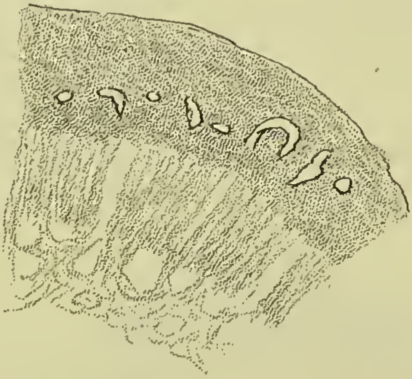
(¹) Decalcified section of tooth of hake. *a.* Formed dentine. *b.* Connective tissue bundles running into it without break of continuity. *c.* Connective tissue framework of the pulp.

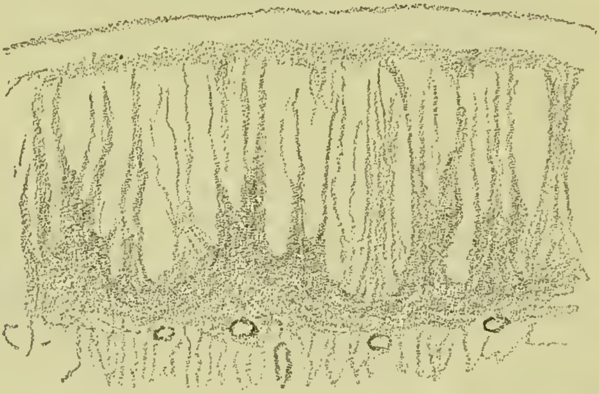
of the pulp, which in vaso-dentine pulps is far more strongly developed than it is in hard dentine pulps. And there being no dentinal tubes to mask it, the dentine can often be seen splitting up in decalcified specimens into bundles of the same size as the fibres of the pulp layer.

Fig. 87 (1).



Moreover, it is much more easy to see the fibres alluded to running into the formed dentine matrix on the one hand, and on the other into the connective tissue deeper in the pulp in vaso-dentine than in hard tubular dentine.

Fig. 88 (2).



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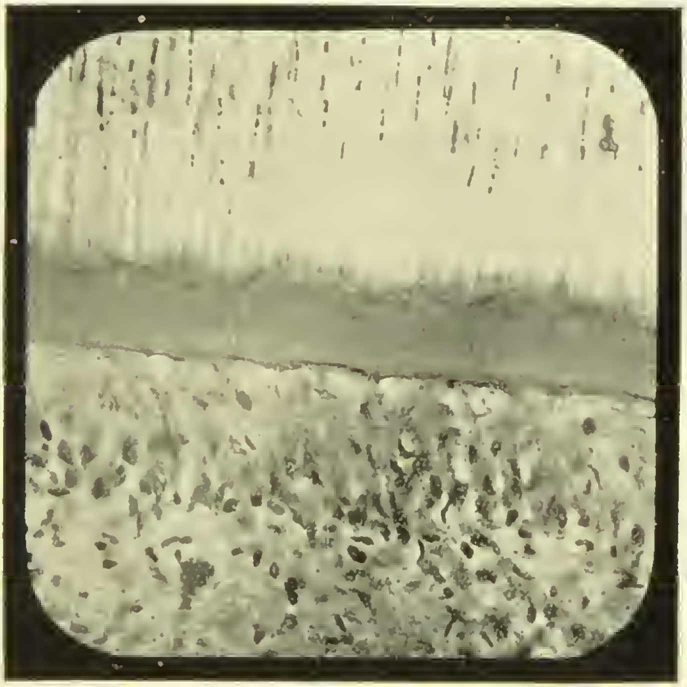
(1) Decalcified section from a hake. The connective tissue fibres are seen forming a layer as distinct as, though greatly thicker than, an odontoblast layer. In the formed dentine the vascular canals are seen, and at the bottom of the figure, the general connective tissue stroma of the pulp.

(2) Outer layer of dentine of a cod.

In the peripheral or first-formed part of the dentine of many vaso-dentine teeth there is a structure which might almost be termed a petrifaction of the connective tissue stroma unchanged. This is well seen in the accompanying figure, drawn from the tooth of a cod. And it cannot be said that there is any fundamental difference between the development of a vaso-dentine and that of hard dentine, for the very same tooth may be composed at one part of the one and at another of the other, as is well exemplified in the tooth of a flounder (see Fig. 40), so that it is quite safe to use the one tissue as illustrating the development of the other.

Fig. 89 (1).



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(1) Developing dentine and pulp from a human tooth, prepared by Weil's process and photographed by Mr. Mummery. Above is seen the completed dentine unstained, but showing the dentinal tubes and fibrils; next is a deeply-stained layer of half-formed dentine, and beneath this again the odontoblasts.

If it then be true, as it appears to be, that the dentine matrix is formed in a connective tissue basis, it becomes a question what share the odontoblasts take in the process. It may be taken as certain that the odontoblast is concerned in the development of the dentinal tubes, keeping them open as it were by its process, the dentinal fibril; and it seems pretty clear that the same odontoblast forms the whole length of the fibril, itself receding backwards as the dentine grows; it seems also possible that it is concerned in the development of the sheaths of Neumann. But inasmuch as Mr. Mummery believes that he has seen other cells applied to the connective tissue fibres, both in man and in fish, if he is right it becomes doubtful whether the odontoblasts are concerned in elaborating the calcifying material.

On the whole, however, their general resemblance to the layers of osteoblasts which clothe the surfaces of developing bone render it probable that they are active agents in the development of the dentine, and we know pretty certainly that dentinal tubes are not formed in their absence, as was well shown by a case recorded by me in the "Transactions of the Odontological Society," 1896.

There is another feature in the development of dentine which has not so far been alluded to, although it is shown in Fig. 89. During the period of active growth of the dentine, but not afterwards, there is a layer between the odontoblasts and the completed dentine, which appears to be in a transitional stage; it usually takes the stain much less deeply, or, in the case of double staining, takes a different colour from that of the rest of the dentine when this has been decalcified. Of course, in sections prepared by Weil's process, it stains more than the dentine, which does not take the stain at all. In this layer an appearance of striation, parallel to the surface of the pulp cavity, can sometimes be seen, and these striæ can be faintly seen in the completed dentine near to it.

In this connection it is interesting to note that decalcified dentine sometimes splits up into laminæ concentric with the pulp, and Mr. F. Bennett noted that in teeth long kept in glycerine, which has a gentle decalcifying action, a similar splitting occurred. The layer of incomplete dentine is, like Neumann's sheaths and the contents of interglobular spaces, stained a deep black by Golgi's method of using nitrate of silver.

The thinnest layer of dentine, such as may be found at the edges of the dentine cap, is soft and elastic, and so transparent as to appear structureless. Where it has attained a somewhat greater thickness, globules begin to appear in it, which are small in the thinner and larger in the thicker portion of the dentine cap. As they are actually in the substance of the cap, their growth and coalescence obviously go on without any very immediate relation to the cells of the pulp; in point of fact, a process strictly analogous to that demonstrated by Mr. Rainie and Professor Harting (see p. 156) is going on. Thus in the formation of the first skin of dentine, a stage of metamorphosis preparatory to impregnation with calcareous salts distinctly precedes that full impregnation which is marked by the occurrence of globules and their subsequent coalescence. The occurrence of these globular forms, and consequent large interglobular spaces, in the deeper parts of adult dentine, is therefore an evidence of arrest of development rather than of any otherwise abnormal condition.

When the formation of the dentine and enamel has gone on to the extent of the crown of the tooth having attained its full length, the reproduction of new formative pulp (in teeth of limited growth) takes place only over a contracted area, so that a neck, and finally one or more roots, are the result of its conversion into tooth substance. In teeth of constant growth, however, no such narrowing of the formative pulp takes place, but the additions to the base of the tooth are of constant or ever-increasing dimensions, as in some tusks, which are thus conical in form.

It is said that the number of roots which would have been developed at the base of a particular dentine organ may be inferred from the vessels, *i.e.*, that in a single-rooted tooth the vessels would, even at an early period, form a single fasciculus; in a double-rooted one, similarly, they would be arranged in two bundles, so that the ultimate formative activity will be exercised around one, two, or three centres of nutrition. I am not, however, able, from my own observations, to throw any light upon this matter.

Dr. Aitchison Robertson found by feeding rabbits with madder that about 1 mm. a week was added to their incisors, but that their molars increased more slowly: the rate of growth of human dentine has not been accurately determined, but the tables of Magitot and of Röse indicate a far slower rate of addition than this.

It seems pretty certain that dentinal tubes once formed are capable of further calcification, by which their calibre becomes sensibly diminished. Thus, my father states (speaking of the incisor teeth of rodents), "the tubes which proceed from the pulp cavity near the base of the tooth are, in most cases, perceptibly larger than those that are situated higher up; hence it follows that, as the latter were once near the base of the tooth, the dentinal tubes undergo a diminution of calibre after their original formation. In the teeth of the Sciuridæ I have found a difference of size amounting to a third or half between the tubes near the base and those near the surface in wear."

And Dr. Lionel Beale calls attention to the fact that the hollows of the canals are larger nearest to the pulp, and smallest at the periphery of the tooth, in other words, at the oldest part; also that calcification is still slowly going on even in advanced life, so as often to lead to the obliteration of the peripheral tubes. There is, too, the statement of Robin and Magitot, that the teeth become more rich in calcareous salts as age advances, so that analyses of human teeth show great discrepancies.

It is difficult to see how a dentinal tube once formed can become contracted to a third or half of its diameter unless we believe that that which was at first the soft tissue (dentinal fibril) occupying its canal may become at its periphery metamorphosed into "dentinal sheath," while that which was originally this latter has passed into the condition of matrix.

But it is very possible that the dentinal sheath has no separate existence in the dentine until after its disintegration by a strong acid.

It has been mentioned (p. 81) that the different varieties of dentine run into one another, and that also dentine in some of its varieties is not distinguishable from bone. The connective tissue theory of the development therefore derives no little support from comparative anatomy, for it brings the development of dentine into line with that of bone, and on the other hand with that of structures very like dentine, which occur in the endo- and exo-skeletons of a great many fish. But other views are still entertained by some authors.

Just as in the case of enamel, there are writers who hold that the odontoblasts are not themselves converted into dentine, but that they preside over the secretion of a material which is. Thus Kölliker and Lent believe that while the canals and their contents are continuations of the odontoblasts, the matrix is a secretion either from these cells or from the rest of the pulp, and so is an "intercellular" substance. Their view is therefore intermediate between the excretion and conversion theories ; and Kölliker goes on to say, "since the dentinal cells are immediately drawn out at their outer ends into the dentinal fibres, and do not, as was formerly thought, grow out in such a manner that the dentinal fibre is to be regarded only as the inner part of the cell, so it is not possible to derive the dentine immediately from the cells." But is not Professor Kölliker thinking and writing of those aged, spent cells which his pupil Lent figured? No one could speak of a young, active odontoblast as "drawn out into the dentinal fibril." A good section of young developing dentine shows that the cells are square and abrupt towards the dentine ; they do not taper into the dentinal process in the smallest degree, and there is little room for any intercellular substance.

Hertz coincides with Kölliker in regarding the matrix as a "secretion from all the dentinal cells in common, which stands in no definite histological relation to the individual cells," but his figure also I believe to be representative of an adult inactive surface of pulp, in which dentine formation has almost ceased.

Kölliker and Lent are of opinion that a single cell is sufficient to form the whole length of a dentinal fibril, not having seen evidence of active cell growth in the subjacent layer of the pulp, from which they could infer that the membrana eboris was supplemented by new cells from below. In a later edition, however, Kölliker speaks with much more hesitation on this point.

Magitot (1881) held that the whole of the dentine is "a product elaborated by the odontoblasts," but neither secreted by nor formed by the conversion of the odontoblasts, and he denied the existence of the sheaths of Neumann *in toto*.

Klein believes that the odontoblast forms the matrix only, whilst the dentinal fibrils are processes continued up between the odontoblasts from a subjacent layer of stellate cells.

Robin and Magitot formerly held that the dentine matrix was formed by the transformation of the odontoblast cells, but that the tubes were *interspaces* between these latter, not corresponding with the axes of the cells.

Baume ("Odontologische Fortschungen") holds that the odontoblasts secrete a material which calcifies, rather than that they are themselves converted.

Of the development of plicidentine nothing need be said, as it is merely the result of the folding up of the formative pulp which proceeds to calcification in just the same way as ordinary fine-tubed dentine.

Calcification of Vaso-dentine.—Like ordinary dentine, this is developed in a uniform layer upon the surface of a simple pulp, which can be pulled out of the cap of formed dentine at any time.

During the calcification of ordinary dentine there is an abundant plexus of capillary vessels a very short distance behind the odontoblast layer, but these recede as dentine formation goes on, and do not, except as a matter of accident, get included in the forming dentine.

Nevertheless, a moment's reflection will show that (except in the earliest stages, before any dentine is formed) this plexus must at a prior time have occupied the place now taken possession of by the inward-marching odontoblasts and dentine.

But in the calcification of a formative pulp into vaso-dentine this recession of its vessels before the advancing border of calcification does not take place; the whole vascular network of the papilla remains and continues to carry blood circulating through it, even after calcification has crept up to and around it.

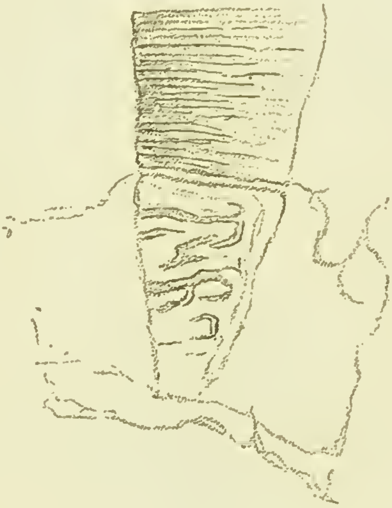
So that if we imagine a vascular papilla to have its stroma suddenly petrified whilst its circulation went on all the same, we should have something like a vaso-dentine.

Just as in a hard dentine, the calcification takes place on the surface of the pulp, but owing to the great development of the connective tissue element the odontoblasts are not so conspicuous, although, by search, round cells like osteoblasts are to be found there.

Indeed, as we have already seen, the very same pulp with an odontoblast layer is able, at the tip of the tooth, to form a finely tubular dentine, and lower down to gradually change its methods so as to leave vessels carrying red blood through special channels. (See Fig. 40.) The typical odontoblasts seem to be concerned in keeping open the tubes of dentine, in which their protoplasmic processes remain, and the study of comparative forms of dentine lends little support to the idea that they are nerve-end organs.

The capability of a pulp to change its method of calcification is very prettily illustrated in the teeth of some fish, of which the Sargus may be selected.

Fig. 90 (¹).



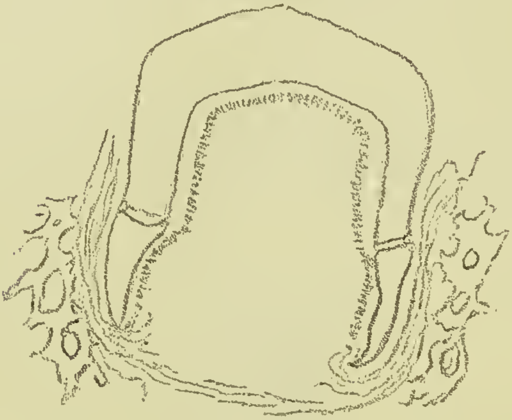
In this fish the dentine pulp for some time goes on forming a fine-tubed hard dentine in which no vascular canals exist, but at a certain point a sudden break occurs, which (Fig. 90) coincides with the commencement of the implanted portion of the tooth.

This implanted portion differs from the true dentine tooth

(¹) Base of the dentine of the crown, and the implanted portion of the tooth. The surrounding bone in which the latter is imbedded is indicated in outline only. (Sargus.)

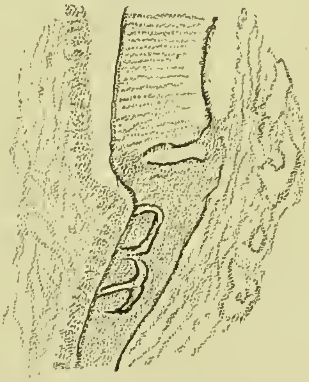
above it, in that it contains at first a few and then none at all of dentine tubes, and it does contain vascular loops and

FIG. 91 ([1]).



the somewhat irregular spaces which are to be found in the bones of these fish.

FIG. 92 ([2]).



Moreover, at the base of the tooth above the break, towards the outer surface of the dentine, a few vascular loops begin to appear, foreshadowing the more complete change which is about to occur.

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[1] Diagrammatic representation of tooth and tooth sac of Sargus, showing the relation of the implanted portion to the odontoblast layer and the tooth sac.

[2] Point of junction of the two portions, more highly magnified.

The great peculiarity of the process is that there is no apparent change in the structure of the formative pulp, which is continued down with its odontoblast layer just the same, not the smallest difference being distinguishable between the pulp above and below the break.

Below it, the tooth pulp with its odontoblast layer goes on forming an additional portion of the same diameter as before, but it is thinned down pretty speedily to an edge.

The after-history of this deeper portion of the tooth is that it is imbedded in and thoroughly fused with the surrounding bone of the jaw.

The Calcification of Osteo-dentine.—With the exception of the thin external layers (see Fig. 46), which are developed from a superficial layer of not very highly specialised cells, osteo-dentine is built up in a manner fundamentally different from that in which hard dentine, plicidentine, and vaso-dentine are constructed.

For it is not, like these, a surface formation; it is not laid down in a regular manner upon the exterior of a pulp, and it has no relation to an odontoblast layer, if we except, perhaps, its thin exterior shell.

So soon as this has been formed, its inner surface becomes roughened by trabeculæ shooting inwards into the substance of the pulp, which speedily becomes traversed completely by them, as well as by the connective tissue bundles which are continuous with them. Thus the pulp, being pierced through in every direction by these ingrowths, cannot be withdrawn, like the pulp of a hard or of a vaso-dentine tooth, from the interior of the dentine cap. Osteoblasts clothe, like an epithelium, the trabeculæ and the connective tissue fibres attached to them, and by the calcification of these the osteo-dentine is formed.

The process is exactly like the calcification of any membrane-bone, and the connective tissue bundles remind one of those which are believed to be the occasion of the formation of Sharpey's fibres in bone. In the case of teeth which are going to be anchylosed to the subjacent bone, these fibres run continuously from the interior of the dentine cap down to the bone, and calcification in and around them binds the two inseparably together.

It is interesting to note, especially in connection with the fact that some observers believe Sharpey's fibres to be elastic, that the hinged teeth of the pike (see Fig. 105) owe their power of resilience entirely to the elasticity of these connective tissue bundles, which do not become completely calcified, although at an early stage it would be quite impossible to say whether a particular tooth was going to be anchylosed, or to be a hinged tooth held up to its work by elastic strings.

Thus it will be seen, that if the connective tissue theory of dentine development be accepted, the development of the several varieties of dentine, which we have already seen to run into one another structurally by almost imperceptible gradations, come into line and so seem more intelligible.

The Calcification of Cementum.—Just as is the case with bones elsewhere in the body, cementum may, perhaps, be formed in two distinct ways—by membranous ossification, and by ossification in a fibro-cartilage, the former method obtaining upon the roots of teeth, and the latter upon those crowns where the cement organ described by Magitot exists.

At the time when the crown of a tooth appears through the gum, it alone is complete, and the root has yet to be calcified ; as each portion of dentine of the root is completed, it is coated with a closely adherent vascular membrane which is, in fact, the follicle wall, and which is to become, when the cement is formed, the alveolo-dental periosteum.

The inner or dentinal face of this membrane presents a layer of large cells, the osteoblasts of Gegenbaur, and it is by their agency that bone or cementum is formed. These osteoblasts are themselves a special development where bone is about to be manufactured, as is clearly explained in the following extract from a paper by my father and the late Mr. De Morgan, who termed them osteal cells :—

"Here (towards the bone) in the place of cells with elongated processes, or cells arranged in fibre-like lines, we find cells aggregated into a mass, and so closely packed as to leave little room for intermediate tissue. The cells appear to have increased in size at the cost of the processes which existed at an earlier stage, and formed a bond of union between them. *Everywhere about growing bone a careful examination will reveal cells attached to its surface, while the surface of the bone itself will present a series of similar bodies ossified.* To these we propose to give the name of osteal cells."

Behind the osteoblasts and very near to the perfect cementum lies a reticulum or network, which looks like connective tissue, and is confused from the interlacing of the processes. Many of these processes pass into, and are lost in the clear, structureless matrix of the already-formed cementum, and persist in it, as Sharpey's fibres.

Where tendons or ligaments are inserted into a bone. the fibres or bundles of the ligament are continued into the bone as penetrating fibres (Sharpey's fibres). Von Ebner holds that they are composed of bundles of fibre-like connective tissue, and thinks that they are not calcified, but merely imbedded in a calcified matrix. It is more commonly thought that in the development of bone, to which cementum is closely similar, bundles of fibres like connective tissue fibre (osteogenic fibres) appear, and become stiffened and calcified by a globular deposition of lime salts in them, these globules coalescing.

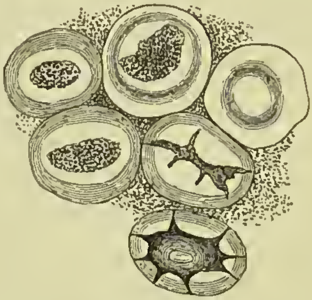
Thus a membrane-bone is at first a network of spiculæ, beyond which extend the as yet soft osteogenic fibres.

Externally to the fine-meshed network which has been well figured and described by Dr. Lionel Beale, the soft tissue surrounding the root partakes more of the character of ordinary fibrous tissue, and may be teased out into fibrils. The fibrous bands run mainly in a direction from the alveolus towards the tooth. Many of them pass through the whole thickness of the soft structures, extending from the bone of the alveolus to the cementum of the tooth, becoming lost at each extremity in the one tissue or the other.

Here and there osteoblasts become enclosed in the forming matrix, and remain as the bone corpuscle of the future bone, occupying its lacunæ.

In carmine-stained preparations from the teeth of calves a round nucleus may sometimes be seen lying in the stellate "lacuna;" the nucleus soon disappears, and plays no active part in determining the form of the lacuna. The nucleus may also be seen in the developing bones of human fœtuses, and, though this is difficult to understand, the traces of the nucleus seem to be beautifully preserved in the lacunæ of a supposed Pterodactyle bone from the Wealden, a section from which was figured by my father in the paper referred to. Exactly as calcification, advancing with irregularity in the interior of an individual cell, fails to render it homogeneous by pervading its whole substance, so it may fail so completely to unite contiguous cells as to obliterate their contours. A lacuna, surrounded by such a contour line, mapping the limits of the original cell, or cluster of cells, is what is termed an "encapsuled lacuna."

Fig. 93 (¹).



That which determines the formation of a lacuna, or an encapsuled lacuna, at any particular spot, is unknown: all that can certainly be said upon the subject is embodied in the following extract from the paper by my father and

---

(¹) Encapsuled lacunæ.
These encapsuled lacunæ are very common in the cementum of the horse, and also in all places where alternations of absorption and deposits have taken place, as in exostosed cementum, "osteoclasts" being very apt to calcify in this way.

Mr. De Morgan, above alluded to: "We see the boundary of the original lacunal cells only in those cases where the lacunæ have but few, or are entirely devoid of canaliculi. It would appear to be a law, to which there are few, if any, exceptions, that when anastomosis is established between adjoining lacunæ, the lacunal cells blend with the contiguous parts, and are no longer recognisable as distinct bodies."

The connective tissue-like fibres are not thought by all histologists to be the primary sources of bone matrix, but some regard the fibrillated ground substance as derived from a part of the osteoblasts. Thus Klein considers that the osteoblasts form both matrix and bone corpuscles. "Each osteoblast by the peripheral portion of its cell substance gives origin to the osseous ground substance, while the central protoplasm round the nucleus persists with the latter as the nucleated bone-cell. The bone-cell and the space in which it lies become branched. For a row of osteoblasts we then find a row of oblong or round territories, each composed of matrix, and in it a nucleated branched cell. The outlines of individual territories are gradually lost, and we have then a continuous osseous lamina, with its bone-cells. The ground substance is from the outset a network of fibrils; it is at first soft, but soon becomes impregnated with inorganic salts, the process commencing at the 'point of ossification.' The bone-cells, with their processes, are situated in corresponding lacunæ and canaliculi, just as in the adult osseous substance."

Professor Schäfer urges as an objection to this view that there is no indication in the formed bone of the cell areas, nor of partly converted osteoblasts; and if the periphery becomes converted into ground substance and the centre and nucleus persist as the contents of a lacuna, the osteoblast should be far larger than the lacuna, which is not the case. This objection, however, applies with less force to the very large "osteoclast" cell, which is as large as the encapsuled lacuna left.

According to Kölliker, the cementum is first deposited in isolated scales, which coalesce with one another, rather than in a continuous sheet. In the teeth of the Primates, the Carnivora, Insectivora, &c., the cementum, at least in any appreciable thickness, is confined to the roots of the teeth.

M. Magitot states that the calcification of his cartilaginous cement organ of Herbivora differs in no respect from that of other cartilages, but in his description he merely states that patches of calcification appear here and there in the deepest portion of the organ, coalesce, and come to invade its entire thickness; and further, that the cement at the period of eruption is constituted of "osteoplasts" regularly grouped round vascular canals, and included in a ground substance finely striated ("Journal de l'Anatomie," 1881, p. 32). But where intra-cartilaginous ossifications occur elsewhere in the body a temporary bone is formed by the calcification of the cartilage matrix, which is subsequently absorbed and swept away, as marrow-containing channels appear in it and bore their way through it, substituting for the calcified cartilage a bone developed from osteoblasts; and ultimately all remains of the calcified cartilage or temporary bone disappear. Thus all bone, whether developed in cartilage or in membrane, is formed alike, the calcified cartilage merely forming a temporary framework or scaffolding, in and amongst which the bone is formed from osteoblasts. But M. Magitot does not describe in any such detail calcification of cartilage and subsequent removal to give place to an osteoblast-derived bone, though he speaks of the cartilaginous cement organ as a transitory or temporary structure.

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THE DEVELOPMENT OF THE JAWS—THE ERUPTION AND THE ATTACHMENT OF THE TEETH.

At an early period in the development of the embryo there is a single primitive buccal cavity, which is subsequently divided into a nasal and an oral cavity by the palatine plates growing horizontally across it; the pharynx behind the hinder end of the primitive buccal cavity remains undivided.

About the third week in the human embryo the foregut (see p. 3) becomes enlarged in the head to form the pharynx. The hyboblast which lines it grows outwards at four different levels, and these outgrowths being met by corresponding ingrowths of the epiblast, four clefts are formed, of which the first is the largest and the fourth the smallest: these go right through, so that they are actual slits.

The tissues intervening between them become thickened and strengthened, so that they form bars between the visceral clefts, and the same thing happens in front of the first and behind the last, so that there are five bars or visceral arches to the four clefts.

In man these clefts are of course transitory structures, but they remain open in fish and most Amphibia, and are familiar to us as the gills of fish, the intervening bars developing vascular filamentous processes, which project into the pharynx and serve for respiration ; the fish takes the aerated water into its mouth and expels it through the slits between its gills or visceral arches.

The visceral arches have, however, an importance to the student of the development of the jaws, for inside the first visceral arch, that is to say, in front of the first visceral cleft, a cartilaginous bar is developed, which runs round to meet its fellow of the opposite side. This is known as Meckel's cartilage ; it starts from the base of the cranium in the immediate neighbourhood of the future ear, and in this end of it two of the auditory ossicles, the incus and malleus, are formed.

The rest of Meckel's cartilage forms a sort of scaffolding, around which the lower jaw or mandible is built up ; but the calcification does not take place in it, as happens with the malleus and incus, for, with the exception of a small piece close to the symphysis, it takes place in the connective tissues outside it.

About the fortieth day a centre of ossification appears in the mandibular process, which, spreading rapidly, soon forms a slight osseous jaw outside Meckel's cartilage, which is not, however, in any way implicated in it, and very soon begins to waste away, so that by the end of the seventh month it has disappeared : that end of it alone which extended up to the tympanum does not so waste away, but becomes ossified into the malleus. There are, however, observers who hold that in some animals, at all events, Meckel's cartilage plays a more active part in ossification of the jaw.

The development of the lower jaw has been accurately described by Mr. Bland Sutton ("Trans. Odontol. Soc.," 1883). After the appearance of Meckel's cartilage, a centre of calcification appears at a point below the future mental foramen, to which the name of the "dentary centre" is given ; then centres appear for the condyle, the coronoid process, the angle, and, at the chin, a mento-meckelian centre.

An osseous network soon connects these, and a splenial calcification appears as a ledge of bone on the inner side of the forming jaw immediately above Meckel's cartilage and the inferior dental nerve. Upon this splenial portion the tooth germs stand "like flasks upon a shelf," then subsequently, as Meckel's cartilage atrophies, the splenial extends downwards to fuse with the dentary, and so cuts off the mylo-hyoid branch of the inferior dental nerve, which branch runs along the groove once occupied by Meckel's cartilage.

It will thus be seen that the centres described by Mr. Bland Sutton correspond pretty closely with the several bones which, though remaining distinct, together go to make up the mandible in Sauropsida ; namely, the articular, angular, dentary, and splenial bones.

The history of the development of the upper jaw is somewhat different. It first appears as a little bud from the base of the first visceral arch, and grows inwards towards the middle line. The primitive buccal cavity or stomodœum (see p. 2) comes to be surrounded by Meckel's cartilage below, the maxillary process at the side, and the fronto-nasal process above.

Thus the upper jaw makes appearance about the twentieth day as a little bud from the first visceral arch, and grows inwards towards the middle line; the processes which form the lower jaw reach to the middle and there coalesce, those for the upper jaw stop short, and the gap left between them is filled by a downward sprouting process from the forehead, which afterwards forms the intermaxillary bone. This naso-frontal process consists of a medium portion and two lateral lobes (processus globulares), from which the upper lip is formed, where they coalesce in the middle line. Their outer edges fuse with the maxillary arches, and it is here that failure of coalescence brings about hare-lip.

In some animals a cartilaginous bar is also developed in the maxillary process, which disappears early.

In the upper jaw the suture separating the intermaxillary from the maxillary bones becomes obliterated very early on the exterior surface, but it remains long distinguishable on the palatine aspect of the bones, where it can be seen up to the fifth year.

According to Albrecht, the intermaxillary bones are developed each from two centres, and for a time there are traces of suture separating these, so that he divides the intermaxillary bone into an "endognathion" and an "exognathion." This is confirmed by Professor Sir William Turner and Biondi. Their anterior surfaces form the alveolar border, *i.e.*, the maxillæ do not come in front of them.

With the later history of the other visceral arches we have not much concern. It will suffice to note that the second cartilaginous bar, called the hyoid bar, arises very close to Meckel's cartilage, and, indeed, has been considered by some anatomists to possibly participate in the formation of the malleus and incus.

The more usual view is, however, that it in great part disappears, but that it is in part converted into the styloid process, stylo-hyoid ligament, and lesser cornu of the hyoid bone. The bar of the third arch, called the thyro-hyoid, in great part also disappears, but its lower end goes to form the greater cornu of the hyoid bone. The student who wishes to pursue this subject further is referred to the very excellent and clear account to be found in the tenth edition of "Quain's Anatomy," by Professor Schäfer.

The later changes which are undergone by the jaws during the development, eruption, and loss of the teeth, have long engaged the attention of anatomists, and amongst others of Hunter, who was the first to arrive at a tolerably correct appreciation of the process. In the first edition of my father's "Dental Surgery," the results of a very extensive series of observations carried out upon maxillæ collected by himself, were detailed, confirming in the main Hunter's conclusions, but adding many new points to our knowledge: and from this work I have borrowed largely in the present chapter. The late Sir G. Humphrey, who had overlooked these descriptions, which were never published in any other form than as an introduction to the "Dental Surgery," instituted a series of experiments upon growing animals, which tended towards the same conclusions.

As a means of giving the student a guide in his reading of the following pages, and a clue to to the results towards which he is being led, a preliminary statement, which does not pretend to scientific accuracy, may perhaps be useful; while the description given will relate for the most part to the lower jaw, because its isolated position, bringing it into relation with fewer other bones, renders it more easy to study; not that any difference of principle underlies the growth of the upper jaw. The different parts of the lower jaw answer for different purposes; one division of its body having a very close and exclusive relation with the teeth, the other serving distinct other purposes, as well as forming a base of support for the dental apparatus.

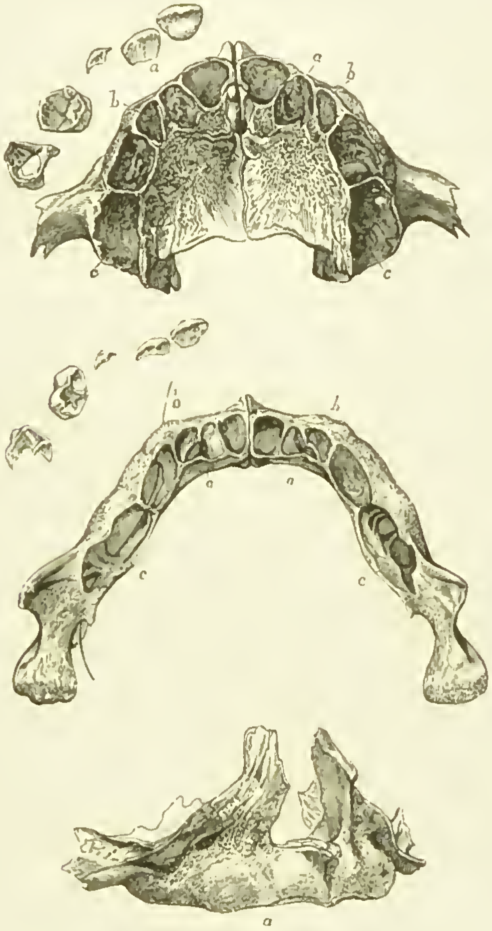
The alveolar portion of the jaw, that which lies above the level of the inferior dental canal, is developed around the milk teeth: when they are lost, it disappears, to be re-formed again for the second set of teeth, and is finally wholly removed after the loss of the teeth in old age.

The portion of jaw below this line, which is essential to deglutition and respiration, is late in acquiring any considerable development. Once formed it is never removed, save that when in advanced old age the muscles of mastication are no longer in full use, it becomes, to a slight extent only, wasted.

In order to understand the drift of the following description, it is essential to keep in view the different life histories of those two parts of the jaw just alluded to.

In an early fœtus, long before the necessity for respiratory movement or deglutition has become imminent, a thin lamina of bone has begun to be formed beneath the tooth germs, forming, as it were, a semicircular gutter running round the jaw, in which the developing tooth sacs are lodged. The

FIG. 94 (1).



thin gutter of bone thus formed is above and outside Meckel's cartilage, and intervenes between the rudimentary inferior maxillary vessels and nerves, and the teeth. The sides of the bony furrow rise as high as the top of the tooth germs, but they do not arch over and cover them in, in such manner as the permanent tooth germs are arched in, for the long furrow is widely open at the top.

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(1) Upper and lower jaws of a nine months fœtus, the teeth having been removed from the jaws on one side to show the extent to which they are calcified at this period. (Two-thirds life size.) *a*. Alveoli of lateral incisors. *b*. Alveoli of canines. *c*. Alveoli of second temporary and first permanent molars. A bristle has been passed through the inferior dental canal.

Passing on to the condition of the mandibles at the time of birth, the two halves are as yet not anchylosed, but are united only by fibro-cartilage. "The alveolar margins are deeply indented with large open crypts, more or less perfectly formed. The depth of these bony cells is only sufficient to contain the developing teeth and tooth pulps, the former rising to the level of the alveolar margins of the jaws. At this period the crypts or alveoli are not arranged in a perfectly uniform line, nor are they all equally complete. The septa, which divide into a series of cells that which at an earlier age was but a continuous groove, are less perfect at the back than at the front part of the mouth. The alveoli of the central incisors of the upper and the lower jaws are a little larger within than at the orifice, and this difference is made still greater by a depression upon the lingual wall of each for the reception of the pulp of the corresponding permanent tooth. They are divided from the crypts of the lateral incisors by a septum which runs obliquely backwards and inwards towards the median line. The sockets for the lateral incisors occupy a position slightly posterior to those for the central teeth, and are divided from the canine alveoli by a septum which proceeds obliquely backwards, and in the lower jaw, as regards the median line of the mouth, outwards. By the arrangement of these divisions the alveoli of the central incisors are rendered broader in front than behind, and these relative dimensions in the sockets of the lateral teeth are reversed, as shown in Fig. 94. The crypts of the canine teeth are placed a little anteriorly to those of the laterals, and nearly in a line with those of the central incisors, giving to the jaws a somewhat flattened anterior aspect."

While the main bulk of the lower jaw is made up by the alveoli of the teeth, in the upper jaw the alveoli descend but little below the level of the palatal plates, though the sockets are tolerably deep. The antrum as a special distinct cavity cannot be said to exist, being merely represented by a depression upon the wall of the nasal cavity, the alveolar cavities therefore being separated only by a thin plate of bone from the orbits.

The figure represents also the extent to which calcification has advanced in the various teeth.

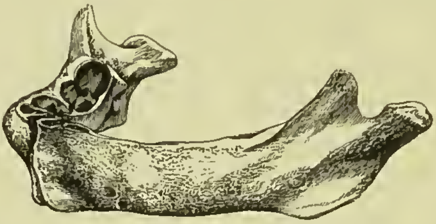
A full half of the length of the crowns of the central incisors, about half that of the laterals, and the tips only of the canines are calcified; the first temporary molars are complete as to their masticating surfaces; the second temporary molars have their cusps more or less irregularly united, in many specimens the four cusps being united unto a ring of dentine, the dentine in the central depression of the crown not being yet formed. During the formation of the permanent teeth, very similar relations exist between the amount of calcification in the incisors and canines; thus when, as sometimes happens, the development of the teeth proceeds very imperfectly up to a certain date, and then changes for the better, it may be that the lower half of the crown of the central incisor, somewhat less of the lateral, and the extreme tip of the canine will be honeycombed, while the remainder of the tooth will be perfect, thus perpetuating an evidence of the stages to which each of these teeth had at that particular period attained.

Having noted in some detail the characters of the jaws of a nine months fœtus, we may pass on to the consideration of those changes which precede the cutting of the deciduous teeth. A general increase in size takes place, new bone being developed at all those points where the maxillæ are connected by soft tissue with other bones, as well as from their own periosteum. But the increase in dimensions does not take place in all directions equally, so that material changes of form result.

In correspondence with the elongation of the tooth sacs, the alveoli become increased in depth, and their edges circle inwards over the tooth sacs; active development of bone takes place in the sutures uniting the two halves of the jaws to one another, which is compensated by the inclination inwards of the alveoli of the central incisors. In the lower jaw the articular process, at first hardly raised above the level of the alveolar border, rises rapidly up, the direction of the ramus at first remaining oblique, though the angle of the jaw becomes developed as a stout process for the attachment of muscles. At the age of six months the symphysis is still well marked, and the mental prominence first becomes noticeable.

An additional bony crypt for the first permanent molar has also appeared, though its separation from that of the second temporary molar, from which it was at first in no way distinct, is yet incomplete, especially in the lower jaw.

FIG. 95 (1).



In the upper jaw the first permanent molar crypt has no posterior wall; bony cells for the permanent central incisors are well marked, but those for the laterals are mere deep pits in the palatine wall of the crypts of the temporary teeth.

At the age of eight months, or thereabouts, the process of the eruption of the teeth, or "teething," has fairly set in; anchylosis has taken place at the symphysis of the lower jaw, the mental prominence is well marked, and in the upper jaw the antrum has become a deep depression, extending under the inner two-thirds of the orbit.

Postponing for the moment the consideration of the eruption of the teeth, in order to follow up the growth of the jaws, it becomes necessary to take some fixed points as standards from which to measure the relative alteration of other portions of the bone. In most bones, processes for the attachment of muscles would be very unsuitable for the purpose, because they would alter with the general alteration in the dimensions of the bone: thus a process situated at a point one-third distant from the articular extremity of a large bone, will still be found one-third distant from the end, though the bone has doubled in length. The four little tubercles which give attachment to the genio-hyo-glossus and genio-hyoid muscles are not, however, open to these objections, as they are already, so to speak, at the end of the bone, or, at least, of each half of it; and their general correspondence in level with the inferior dental canal, which can hardly be imagined to undergo much alteration, indicates that their position is tolerably constant.

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(1) Lower jaw of a nine months fœtus.

The points selected as landmarks are then, the spinæ mentales, the inferior dental canal and its orifice, and the mental foramen. The mental foramen itself does undergo slight change in position, but this change can easily be estimated, and may as well at once be mentioned. As the jaw undergoes increase in size, large additions are made to its surface by deposition of bone from the periosteum, necessarily lengthening the canal. The additions to the canal do not, however, take place quite in the line of its original course, but in this added portion it is bent a little outwards and upwards. If we rasp off the bone of an adult jaw down to the level of this bend, a process which nature in great part performs for us in an aged jaw, or if instead we make due allowance for the alteration, the mental foramen becomes an available fixed point for measurement.

The mental foramen, which undergoes most of its total change of position within a few months after birth, comes to correspond with the centre of the socket of the first temporary molar; later on it corresponds with the root of the first bicuspid, which is thus shown to succeed, in exact vertical position, the first temporary molar.

On the inner surface of the jaw the tubercles for the attachment of the genio-hyo-glossus and genio-hyoid muscles are in the fœtus, opposite to, and very little below the base of the alveoli of the central incisors, a position which they afterwards hold with regard to the permanent incisors. The upper of the two pairs of processes are about at the same general level as the mental foramen.

The general result arrived at by measurements taken from these fixed points is that the alveolar arch occupied by the teeth which have had deciduous predecessors, namely the incisors, canines, and bicuspids, corresponds very closely with the whole alveolar arch of the child in whom the temporary dentition is complete; and that the differences which do exist are referable, not to any fundamental alteration in form or interstitial growth, but to mere addition to its exterior surface. Or more briefly, that the front twenty of the permanent succeed vertically to the places of the temporary teeth, the increase in the size of the jaw in an adult being due to additions at the back, in the situation of the true molars, and to other points on the surface.

If measurements be taken across between the inner plates of the alveoli on either side at the points where they are joined by the septa between the first and second temporary molars, and at about the level of the genio-hyo-glossus tubercles, it will be found that the increase is slight, if any, notwithstanding that in other dimensions there is a very great difference between the jaws of a nine months fœtus and of a nine months child.

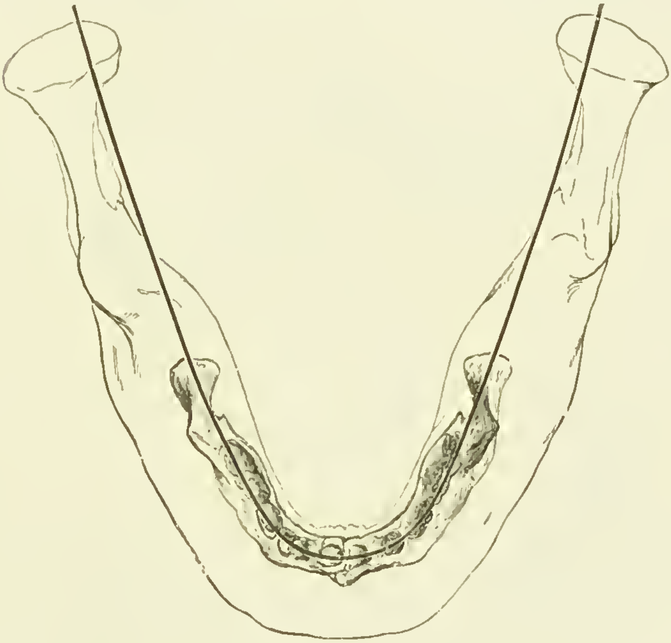
Again, if an imaginary line be stretched across between these two points, and from its centre a line be drawn forwards to the spina mentalis in the same two jaws, this will be found to differ but little in length in the two specimens.

But, if instead of measuring to the spina mentalis, the line had been carried to the anterior alveolar plate, a great difference would have been observable; in point of fact, contemporaneously with the development of the crypts of the permanent teeth inside them, the temporary teeth and their outer alveolar plates are slowly pushed outwards, a process, the results of which we see in the separation which comes about between each one of the temporary teeth, prior to their being shed, when the process of dentition is being carried on in a perfectly normal manner.

Measurements taken for the sake of comparing adult jaws with those of an eight months child, give closely similar results, which I have endeavoured to roughly embody in the accompanying figures.

In these it is shown that the increase in the dimensions of the jaw has taken place in two directions; by prolongation backwards of its cornua concomitantly with the addition at the back of the series of teeth of the true molars, which follow one another at considerable intervals; and by additions to its exterior surface by which it is thickened and strengthened. The study of the growth of the jaw in vertical depth is also very instructive. We find that, as

Fig. 96 (¹).

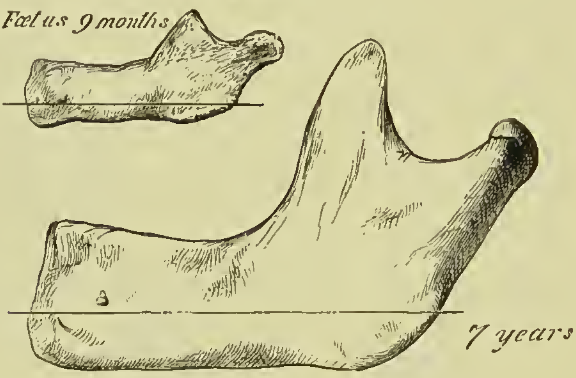


(¹) Diagram representing a jaw of a nine months fœtus, superimposed upon an adult jaw, to show in what directions increase has taken place.

has already been mentioned, the history of that part of the jaw which lies below the inferior dental canal is very different from that which lies above. From the time of birth to that at which the temporary teeth begin to be cut, the jaw below that line has been making steady but slow progress in vertical depth; the alveoli, above that line, have been far more active but far more intermittent in their development.

Again, passing from the nine months fœtus to the seven years old child, in whom the temporary dentition is complete, the framework of the jaw below our imaginary line has attained to a depth almost equal to that which it is seen to have in an adult; in the adult again it corresponds pretty well with that in an aged jaw. The alveolar portion, however, is far deeper in the adult than in the child (this difference is not sufficiently well marked in the figure), and in fact constitutes almost the whole increase in vertical dimensions during the passage from the child's to the adult's form of the jaw.

FIG. 97 (1).



In the lower jaw we may then take it as proven that the basal portion has little relation to the development of the teeth, but that the alveolar, or upper portion is in entire and absolute dependence upon them, a point to which I shall again return in speaking of the eruption of the teeth.

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(1) Lower jaw. The horizontal line marks the level of the inferior dental canal.

It remains to speak in some further detail of the precise means by which the enlargement of the jaw is effected.

To a slight extent there is formation of bone going on at the symphysis, prior to the complete anchylosis taking place; the share taken by this in increasing the size of the jaw would, however, appear to be but small, after the termination of the intra-uterine period. Additions to the surface,

Fig. 98 (1).

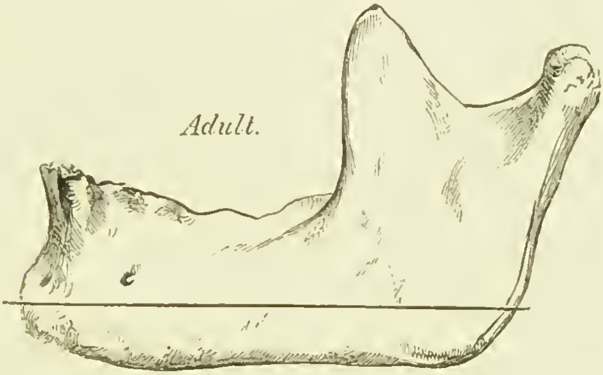
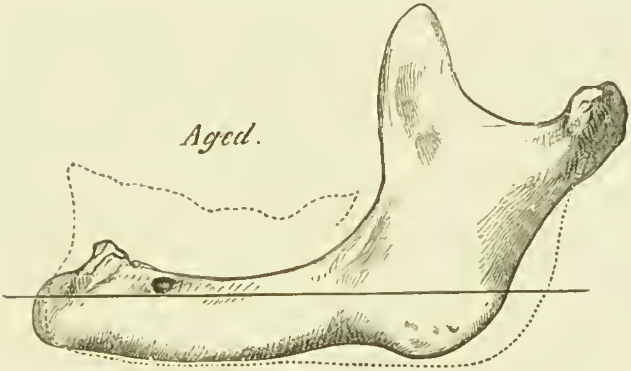


Fig. 99 (2).



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(1) Lower jaw of an adult.

(2) Lower jaw of an aged person, the dotted lines indicating the outline of the parts removed by absorption, as the jaw assumes the form characteristic of advanced age.

at the edges of the alveoli and at the base of the jaw are continually going on, and bring about that addition to the exterior already noticed.

But the main increase in the size of the jaw has been in the direction of backward elongation; in this, as Kölliker first pointed out, the thick articular cartilage plays an important part. The manner in which the jaw is formed might also be described as wasteful; a very large amount of bone is formed which is subsequently, at no distant date, removed again by absorption; or we might compare it to a modelling process, in which thick, comparatively shapeless masses, are dabbed on to be trimmed and pared down into form.

To bring it more clearly home to the student's mind, if all the bone ever formed were to remain, the coronoid process would extend from the condyle to the region of the first bicuspid, and all the teeth behind that would be buried in its base: there would be no "neck" beneath the condyle, but the internal oblique line would be a thick bar corresponding in width with the condyle. It is necessary to fully realise that the articular surface with its cartilage has successively occupied every spot along this line; and as it progresses backwards by the deposition of fresh bone in its cartilage, it has been followed up by the process of absorption removing all that was redundant.

On the outer surface of the jaw we can frequently discern a slight ridge, extending a short distance from the head of the bone; but if the prominence were preserved on the inner surface, the inferior dental artery and nerve would be turned out of their course. We have thus a speedy removal of the newly-formed bone, so that a concavity lies immediately on the inner side of the condyle; and microscopic examination of the bone at this point shows that the lacunæ of Howship, those characteristic evidences of absorption, abundantly cover its surface, showing that here at least absorption is most actively going on.

In the same way the coronoid process, beneath the base of which the first, second, and third molars have successively been formed, has moved backwards by absorption acting on its anterior and deposition on its posterior surfaces.

The periosteum covering the back of the jaw is also active in forming the angle and the parts thereabouts.

It is worth while to add that the direction of growth in young jaws is marked by a series of minute ridges; in like manner the characteristic marks of absorption are to be found about the neck of the condyle, and the front of the coronoid process, and those of active addition about the posterior border, so that the above statements rest upon a basis of observation, and are not merely theoretical. Two cases of arrested development of the jaw ("Dental Surgery," 4th Ed., p. 57) lend a species of experimental proof to the theory of the formation and growth of the jaw above given.

There are authors, however, who maintain that the growth of the jaws is not merely a backward elongation of the cornua, together with additions to the external surface, but that an "interstitial growth" takes place.

Wedl inclines to this latter view, and the question cannot, I think, be held to be absolutely settled. Although it is difficult to form any definite conception of interstitial growth in a tissue so dense and unyielding as bone, so that the doctrines promulgated in the foregoing pages have the support of *à priori* probability, there are some rather paradoxical facts to be met with in comparative odontology. Nevertheless, there can be no doubt that backward elongation as teeth are successively added, &c., is sufficiently near the truth in the case of human and most mammalian jaws for practical purposes.

In the museum of the Royal College of Surgeons there is a series of models of the same mouth from the age of four up to the age of twenty-one, which I carefully examined ("Trans. Odontol. Soc.," 1892), with the result of fully confirming the conclusions arrived at in the foregoing pages, and I further instituted a comparison with the jaws of certain of the anthropoid apes.

In these latter the same conclusions as to the absence of growth in the region occupied by the temporary teeth do not hold good, as during the change from the temporary to the permanent dentitions there is a large antero-posterior elongation.

But this elongation takes place almost entirely in the extent of the intermaxillary bones, and is much greater in the orang and the gorilla than in the chimpanzee; and this difference appears to correspond with, amongst other things, the date of the closure of the intermaxillary suture, which takes place much earlier in the chimpanzee than in the other two genera of anthropoid apes, and seems to bear a proportion to the extent of development of the canines.

Thus a large part of the prognathism of these apes is due to long-continued growth in the intermaxilla, and it would be very interesting to ascertain if the prognathism of the lower races of mankind is also due to the obliteration of the suture being deferred longer than in the European races; but, unfortunately, the material for this investigation does not appear to exist in this country.

It remains to notice the changes in form which the ascending ramus and the angle of the jaw undergo. In the fœtus the ramus is but little out of the line of the body of the jaw, and the condyle little raised above the alveolar border.

Gradually the line of development, as is indicated even in the adult jaw by the course of the inferior dental canal, takes a more upward direction; copious additions of bone are made on the posterior border and about the angle, so that in an adult the ramus ascends nearly at right angles to the body of the jaw.

In old age, concomitantly with the diminution of muscular energy, the bone about the angle wastes, so that once more the ramus appears to meet the body at an obtuse angle. But all the changes which mark an aged jaw are the simple results of a superficial and not an interstitial absorption, corresponding with a wasting of the muscles, of the pterygoid plates of the sphenoid bone, &c.

ERUPTION OF THE TEETH.

The mechanism by which teeth, at the date of eruption, are pushed upwards into place is far from being perfectly understood. The simplest theory would appear to be that they rise up, in consequence of the addition of dentine to their base; in fact, that their eruption is due to the elongation of their roots.

Various very strong objections have been brought forward, clearly proving that this cause is quite inadequate to explain all that may be observed. In the first place, teeth with very stunted roots—which, may be practically said to have no roots—are often erupted. Again, a tooth may have the whole length of its roots completed, and yet remain buried in the jaw through half a person's life, and then, late in life, be erupted. Moreover, when a healthy normal tooth is being erupted, the distance travelled by its crown often greatly exceeds the amount of addition to its length which has gone on during the same period.

To turn to comparative anatomy, the tooth of a crocodile moves upwards, tooth pulp and all, obviously impelled by something different from mere elongation; and my own researches upon the development and succession of reptilian teeth clearly show that a force quite independent of increase in their length shifts the position of and "erupts" successive teeth.

It has been suggested by Mr. Constant ("Journal British Dental Association," 1896) that the blood pressure may be the impelling force, the pulp and tissues beneath the tooth being more rich in their vascular supply than those above it.

It seems very possible that the blood pressure keeping up a state of general tension may operate to push a solid body in any direction in which there is a diminished resistance, to take up, so to speak, any unoccupied place; but it is difficult to see how it could be efficient without some such concomitant action of absorption. For the movement of an erupting tooth is not always by any means in the direction of its long axis; for instance, the developing tooth of the frog, the newt (Figs. 70 and 125), or of the crocodile takes a sideway journey, by which it travels underneath the old tooth, before it moves upwards at all.

But if its path be prepared by absorption of the structures in its way, then it is very possible that the blood pressure keeping up a certain general tension may suffice to move it along a track of diminishing resistance. Mr. Constant's suggestion, with a little modification, is the most plausible that has been offered, therefore, as to the actual motive force : whether it will be regarded as a final solution of the question time alone can show.

In man, towards the eighth month of childhood the bony crypts which contain the temporary teeth in the front of the mouth begin to be removed. The process of absorption goes on with greater activity over the fronts of the crowns than over their apices, so that almost the whole outer wall of the alveoli is removed. At the back of the mouth the crypts still retain their inverted edges; indeed, development of the crypts is still going on in this part of the mouth.

When a tooth is about to be cut, very active absorption of its bony surroundings goes on, particularly on the anterior surface, the bone behind it being still required as forming part of the crypt of the developing successional tooth. But no sooner has the crown passed up through the very wide and free orifice so formed than absorption gives place to deposition, and the bone rapidly develops so as to loosely embrace the neck of the tooth.

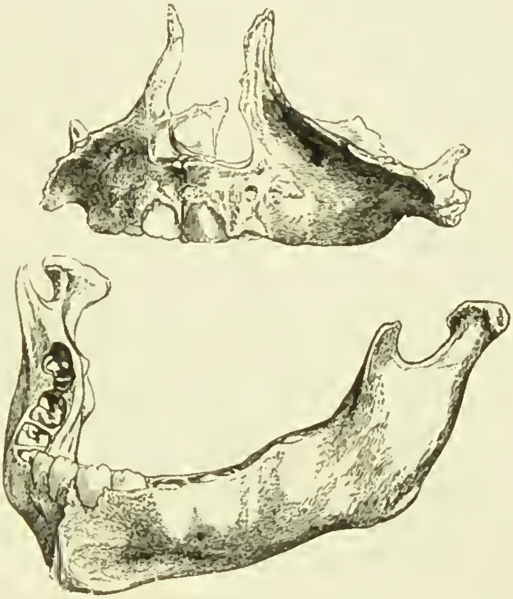
Additions to the margin of the alveoli keep pace with the gradual elongation of the roots of the teeth; as this is a moderately rapid process, the alveolar portion of the jaw increases in depth almost abruptly.

But it does not do so uniformly all over the mouth ; if it did, the teeth could only be closed at the back of the mouth, unless the rami elongated by an equally sudden accession of new bone.

The front teeth are erupted first, and the jaw deepens first in front; later on the back teeth come up and the jaw is deepened posteriorly; meanwhile the elongation of the rami has been going on slowly, but without interruption. Thus is brought about a condition of parts allowing of the whole series of teeth coming into their proper mutual antagonism.

It was pointed out by Trousseau that the eruption of the teeth is not a continuous process, which, once commenced, is carried on without intermission to its completion, but that it is interrupted by periods of repose. The teeth are, according to his statement, cut in groups; the eruption of the teeth of each group being rapid, and being succeeded by a complete cessation of the process. Individual variations are numerous; the following may be taken as an approximation to the truth:—

Fig. 100 (¹).



The lower centrals are erupted at an age ranging from six to nine months; their eruption is rapid, and is completed in ten days or thereabouts; then follows a rest of two or three months.

(¹) Jaws of a male nine months old, in which the eruption of the teeth is just commencing.

Next come the four upper incisors ; a rest of a few months ; the lower laterals and the four first molars ; then a rest of four or five months.

The canines are peculiar in being the only teeth of the temporary set which come down between teeth already in place. To this, as well as to the greater length of their root (although it is not quite clear what this has to do with it), Trousseau ascribes the great length of time which their eruption occupies, it taking two or three months for its completion. According to him, children suffer more severely from constitutional disturbance during the cutting of these teeth than that of any other, but Dr. West thinks that the eruption of the first molars causes the most suffering. It may also be noted that the canines during their development lie farther from the alveolar border than do the other teeth, so that they travel a greater distance ; obviously, not merely from the elongation of the root, which is wholly inadequate to effect such a change in position.

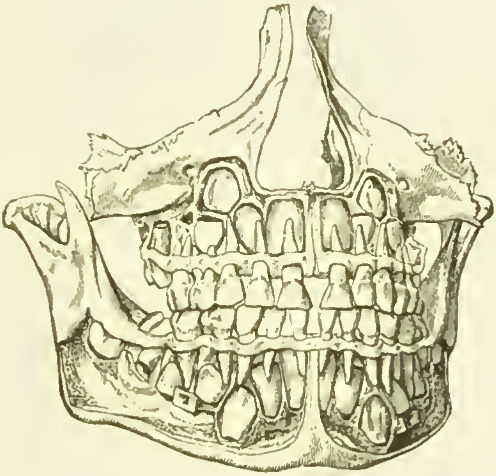
The dates of the eruption of the milk teeth vary much, no two authors giving them alike ; but the whole of the deciduous teeth are usually cut by the completion of the second year. Cases in which incisors have been erupted before birth are not very uncommon. At a time when the crowns of all the deciduous teeth have been fully erupted, their roots are still incomplete, and are widely open at their bases, so that it is not till between the fourth and sixth years that the temporary set of teeth can be called absolutely complete.

At the sixth year, preparatory to the appearance of any of the permanent teeth, the temporary teeth may be observed to be slightly separated from each other ; they have come to occupy a more anterior position, pushed forward, it may be, by the great increase in size of the crypt of the permanent teeth behind them. The general relation of these to the temporary teeth may be gathered from the accompanying figure, in which it will be noticed that the canines lie far above and altogether out of the line of the other teeth, and that a slight degree of overlapping of the edges of the permanent central and lateral incisors exists.

The bicuspids lie in bony cells which are embraced pretty closely by the roots of the temporary molars, and it hence happens that extraction of these latter sometimes brings them away in their entirety.

The first permanent molars are erupted in a manner closely similar to that described as occurring with the temporary teeth; that is to say, their bony crypts become widely opened out by absorption, the crown passes out, and new bone is rapidly formed which loosely embraces the neck, prior to any considerable length of root being formed.

FIG. 101 (¹).

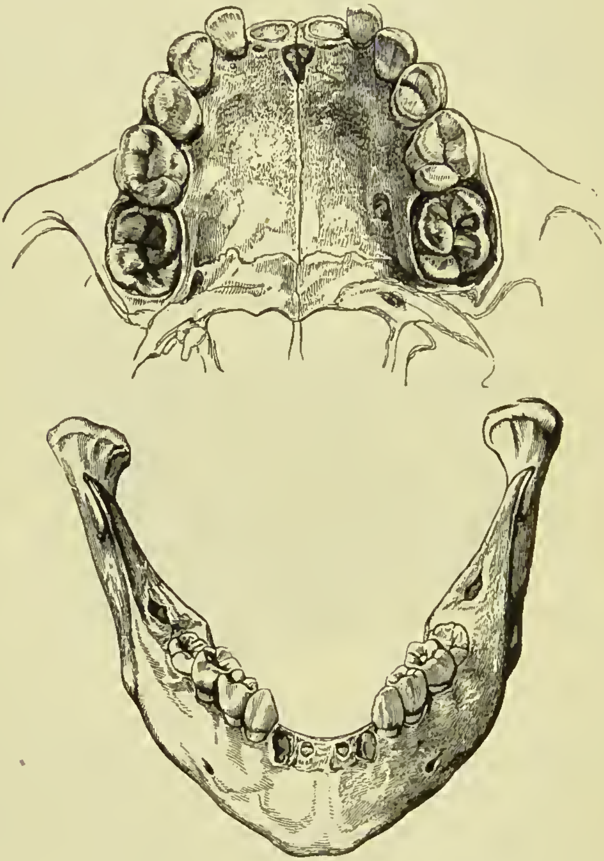


Last, then, follows the absorption of the root of the temporary teeth, a matter first accurately investigated by my father. The root at or near to its end becomes excavated by shallow cup-shaped depressions; these deepen, coalesce, and thus gradually the whole is eaten away. Although absorption usually commences on that side of the root which is nearest to the successional tooth, it by no means invariably does so; it may be, and often is, attacked on the opposite side, and in many places at once.

(¹) Normal well-formed jaws, from which the alveolar plate has been in great part removed, so as to expose the developing permanent teeth in their crypts in the jaws.

The cementum is usually attacked first, but eventually dentine, and even enamel come to be scooped out and removed by an extension of the process. That part of the dentine, however, which immediately surrounds the pulp appears to have more power of resistance than any other part of the tooth, and thus often persists for a time as a sort of hollow column. The absorption of the temporary teeth is absolutely independent of pressure ; the varying position of the excavation has already been noticed, and it may be

Fig. 102 (1).



(1) Jaws of a six-year old child. In the upper jaw complete sockets are seen where the temporary incisors have been shed.

added that in many lower animals, for example, the frog or the crocodile, the growing tooth sac passes bodily into the excavation made before it in the base of the tooth which has preceded it, while if pressure had had any share in the matter the cells of its enamel organs, &c., must have inevitably been crushed and destroyed.

Again, when the absorption and shedding of the first teeth have taken place early, before their successors are ready to appear, perfect little sockets are formed behind the lost temporary teeth, cutting them off from the permanent teeth destined to follow them. Absorption, too, may attack the roots of permanent teeth, which is another reason for regarding the process as not necessarily dependent upon the approach of a displacing tooth. Closely applied to the excavation produced by absorption is a mass of very vascular soft tissue, the so-called absorbent organ. The surface of this is composed of very large peculiar-looking cells, bearing some little resemblance to those known as "myeloid cells," or the "giant cells" of recent authors. Microscopic examination of the excavated surface shows it to be covered with small hemispherical indentations, the "lacunæ of Howship," into each of which one of the giant cells was fitted, and in which they may sometimes be seen *in situ*.

In what manner these giant cells, or "osteoclasts," effect their work is not known, but their presence where absorption of hard tissues is going on is universal. Some suppose that they put forth amœbiform processes, others that they secrete an acid fluid, but nothing very definite is known; a curious parallel is afforded by the manner in which a fungus can drill and tunnel through and through the dentine, as may be very constantly observed in teeth long buried.

The process of absorption once commenced does not necessarily proceed without intermission, but may give place for a time to actual deposition of osseous tissue on the very surface eroded; probably by the agency of the absorbent cells themselves, which are capable of being calcified in the excavations they have individually made.

These alternations of absorption and deposition, so common a result of inflammations of the pulp or of the alveolo-dentar periosteum, as to be diagnostic of the former occurrence of these maladies, often occur during the normal process of the removal of the deciduous teeth, and result in the deposition of a tissue not unlike cementum in excavations made in the dentine, or even in the enamel.

The eruption of the permanent teeth is a process closely analogous to that of the temporary set. Rapid absorption of the bone, especially on the exterior surface of the crypts, takes place, and an orifice very much larger than the crown of the tooth is quickly opened out.

Hence it is that the slightest force will suffice to determine the direction assumed by the rising crown: a fragment of a root of a temporary tooth, the action of the lips and tongue, &c., are all potent agencies in modifying the arrangement of the teeth.

The temporary teeth stood vertically, the permanent teeth in front of the mouth stand obliquely, thus opening a space between the lateral incisors and the first bicuspid for the canine, which during development was out of the line altogether. And, inasmuch as the crowns of the teeth are on the whole much larger than their necks, it would be manifestly impossible for them all to come down simultaneously.

The permanent teeth usually make their appearance in the following order:—First permanent molars, about the seventh year; a little later, the lower central incisors, upper centrals and laterals, the first bicuspids, the canines, the second bicuspids, the second permanent molars, the third permanent molars.

The period of eruption is variable. From a comparison of several tables, I find the principal discrepancies to relate to the date of the appearance of the canines and the second bicuspids. The canine would certainly appear to belong to the eleventh and twelfth years; but some authors consider that the second bicuspid is usually cut earlier, others later than this date.

We may now revert to the phenomena observed in the alveolar processes. They were first built up as crypts with overhanging edges enclosing the temporary teeth ; then they were swept away, in great part, to allow of the eruption of the temporary teeth ; and next they were rebuilt about their necks, to form their sockets.

Once more, at the fall of the deciduous teeth, the alveoli are swept away, the crypts of the permanent teeth are widely opened, and the permanent teeth come down through the gaping orifices.

When they have done so, the bone is re-formed so as to closely embrace their necks, and this at a period when but little of the root has been completed.

Take for example the first upper or lower molars : their short and widely-open roots occupy the whole depth of the sockets, and reach respectively nearly to the floor of the antrum and the inferior dental canal. No growth, therefore, can possibly take place in these directions ; the utmost available depth has already been reached, and as the roots lengthen the sockets must be deepened by additions to their free edges.

It is impossible to insist too strongly upon this fact, that the sockets grow up with and are moulded around the teeth as the latter elongate. Teeth do not come down and take possession of sockets more or less ready made and pre-existent, but the socket is subservient to the position of the tooth ; wherever the tooth may chance to get to, there its socket will be built up round it.

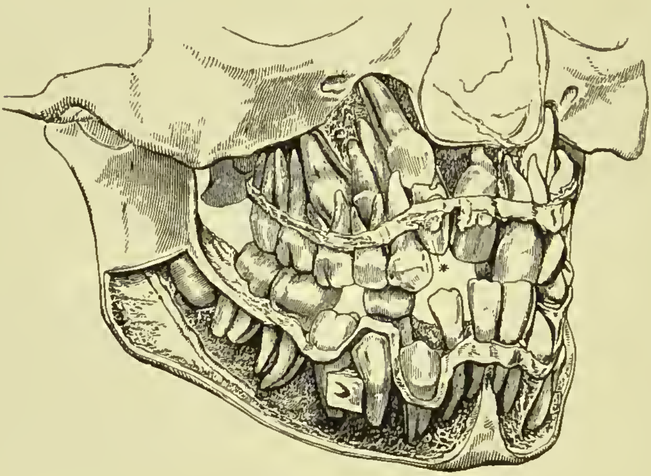
Upon the proper appreciation of this fact depends our whole understanding of the mechanism of teething ; the position of the teeth determines that of the sockets, and the form of the pre-existent alveolar bone has little or nothing to do with the disposition of the teeth.

During the period of eruption of the permanent teeth the level of the alveolar margin is seen, in a dried skull, to be extremely irregular, the edges of the sockets corresponding to the necks of the teeth, whether they have attained to their ultimate level, or have been but just cut.

And when temporary teeth have been retained for a longer period than is natural, they sometimes become elevated to the general level of the permanent teeth (which is considerably higher than that of the temporary teeth), so that they take their share of work in mastication. When this is the case the alveoli are developed round them, and come to occupy with their tooth a higher level than before.

Enough has perhaps been said to illustrate the entire dependence of the alveoli upon the teeth, a relation of which dentists every day avail themselves in the treatment of regulation cases: it remains to say a few words as to the forces which do determine the position of the teeth.

FIG. 103 (¹).



Inasmuch as when a tooth leaves its bony crypt, the bone does not at first closely embrace it, but its socket is much too large for it, a very small force is sufficient to deflect it. And, indeed, a very slight force, constantly operating, is sufficient to materially alter the position of the tooth, even when it has attained to its full length.

Along the outside of the alveolar arch the muscular lips

(¹) From a child aged fourteen. The specimen well exemplifies the fact that the height of the alveolar edge corresponds exactly to the position of the neck of each tooth, on which it is wholly dependent. A temporary tooth (the first right lower temporary molar) has been elevated, so that it has attained to the level of the surrounding permanent teeth, and the edge of the socket follows the level of the neck of the tooth.

are exercising a very symmetrical and even pressure upon the crowns of the teeth; so also the tongue, with equal symmetry, is pushing them outwards: between the two forces, the lips and the tongue, the teeth naturally become moulded into a symmetrical arch.

When the crowns of the teeth have attained such a level as to come in contact with their opposing teeth, they very speedily, from readily intelligible mechanical causes, are forced into a position of perfect correspondence and antagonism; and even at a somewhat later period than that of eruption, if this antagonism be interefred with, the teeth will often rise up so as to readjust themselves in position.

CHAPTER VI.

THE ATTACHMENT OF TEETH.

Although the various methods by which teeth are fixed in their position upon the bones which carry them pass by gradational forms into one another, so that a simple and at the same time absolutely correct classification is impossible, yet for the purposes of description four principal methods may be enumerated, namely, attachment by means of fibrous membrane, by a hinge, by anchylosis, and by implantation in bony sockets.

Attachment by means of Fibrous Membrane.—An excellent illustration of this manner of implantation is afforded by the Sharks and Rays, in which the teeth have no direct connection with the cartilaginous, more or less calcified jaws, but are imbedded solely in the tough fibrous mucous membrane which covers them. This, carrying with it the teeth, makes a sort of sliding progress over the curved surface of the jaw, so that the teeth once situated at the inner and lower border of the jaw, where fresh ones are constantly being developed, rotate over it, and come to occupy the topmost position (cf. description of the dentition of the sharks). That the whole fibrous gum, with its attached teeth, does really so slide over the surface of the jaw was accidentally demonstrated by the result of an injury which had been inflicted upon the jaws of a shark.

The fibrous bands by which each individual tooth of the shark is bound down are merely portions of that same sheet of mucous membrane which furnished the dentine papillæ; and the gradual assumption of the fibrillated structure by that portion of the mucous membrane which is contiguous to the base of the dentine papilla may be traced, no such fibrous tissue being found at the base of young papillæ, and very dense bands being attached to the bases of the completed calcified teeth.

A large number of fish have their teeth attached to short pedestals of bone by means of a sort of annular ligament, which allows of a slight degree of mobility. This would seem to be the case in many of those whose teeth have been generally supposed to be anchylosed, such as the sargus (cf. Fig. 91 and Fig. 92), although in the completed tooth the joint is so close that only an inspection of the developing tooth gives a hint as to the true nature of the attachment.

By the limitation of this ligament to one side, where it is greatly strengthened, we pass by easy transitions to those more specialised arrangements characteristic of hinged teeth.

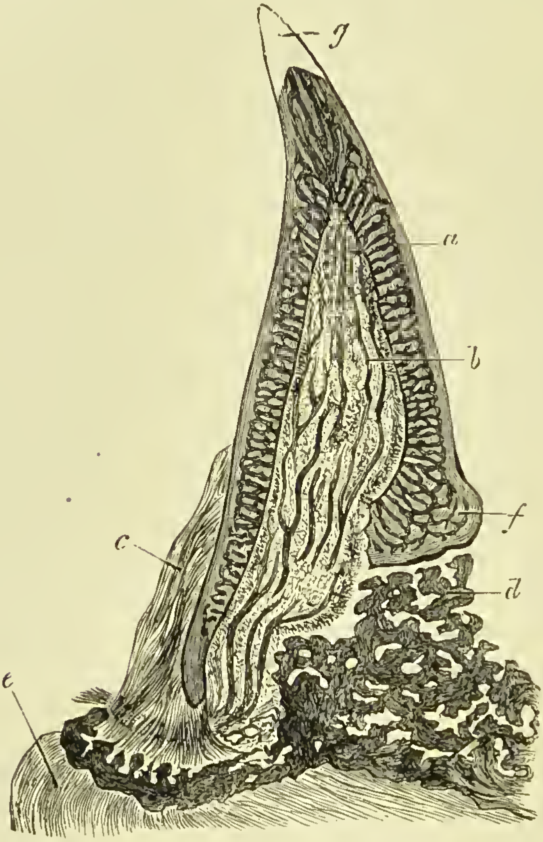
Attachment by an Elastic Hinge.—The possession of moveable teeth, able to yield to pressure, and subsequently to resume the upright position, was formerly supposed to be confined to the Lophius (Angler) and its immediate allies. I have, however, found hinges in the common pike (Esox), and in the Gadidæ (Cod tribe); so that, as they occur in these fish so widely removed from one another in other respects, it is probable that further investigation will bring, and, indeed, is bringing, to light many other examples of this very peculiar method of attachment, eminently suited to, and hitherto only discovered in, fish of predatory habits.

In the Angler, which obtains its food by lying in ambush on the bottom, to which it is closely assimilated in colour, many of the largest teeth are so hinged that they readily allow an object to pass into the mouth, but, rebounding again, oppose its egress. These teeth are held in position by dense fibrous ligaments radiating from the posterior side of their bases on to the subjacent bone, while the fronts of the bases of the teeth are free, and, when the teeth are pressed towards the throat, rise away from the bone. The elasticity of the ligament is such that when it has been compressed by the tooth bending over towards it, it returns it instantly into position with a snap. Many of the teeth of the Angler are, like most fishes' teeth, anchylosed firmly.

The Hake (Merlucius, one of the Gadidæ) possesses two rows of teeth, the outer and shorter of which are anchylosed, while the inner and longer are hinged.

In some respects these hinged teeth are more highly

FIG. 104 (1).



specialised than those of the Angler, which they resemble in being attached by an elastic hinge fixed to their inner sides, the elasticity of which is brought into play by its being compressed, or, at all events, bent over upon itself.

(1) Hinged tooth of hake. *a.* Vaso-dentine. *b.* Pulp. *c.* Elastic hinge. *d.* Buttress of bone to receive *f*, formed out of bone of attachment. *e.* Bone of jaw. *f.* Thickened base of tooth. *g.* Enamel tip.

The pulp is highly vascular, and its vessels are so arranged that, by entering the pulp through a hole in the ligament, which is about at the axis of motion, they escape being stretched or torn during the movements of the tooth. And the free edge of the base of the tooth itself is modified so as to be particularly fitted for resisting the jars to which a moveable tooth must at times be exposed, and so is the pedestal of bone upon which it strikes.

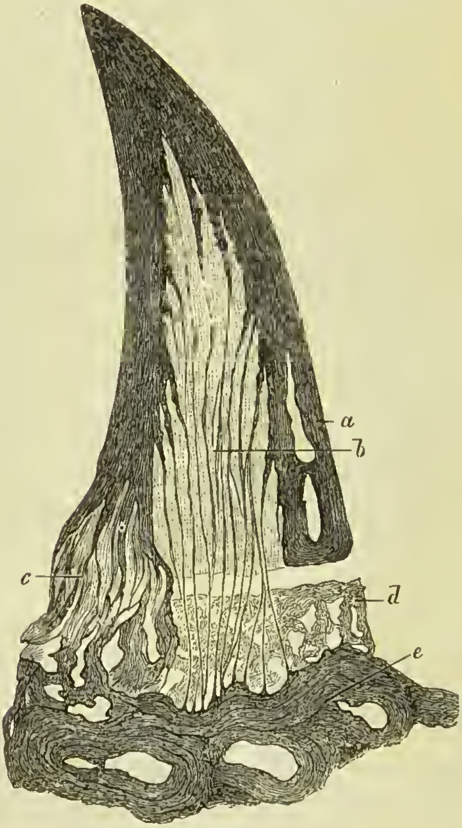
As is seen in the figure, the base of the tooth, on the side opposite to the hinge, is thickened and rounded, the advantages which such a form must possess over a thin edge when bumping upon the bone being sufficiently obvious. This thickened edge is received upon a little buttress of bone, and it occupies a much higher level than the opposite thin edge to which the hinge is attached, so that the tooth cannot possibly be bent outwards without actual rupture of the ligament.

And what is not a little remarkable is, that whilst the Hake, the most predatory of all the Gadidæ, is possessed of these very perfectly hinged teeth, other members of the family have teeth moveable in a less degree, whilst others again have teeth rigidly fixed. So that within the limits of a single family we have several steps in a gradual progression towards a very highly specialised organ.

In the hinged teeth already alluded to the purpose served by their mobility seems to be the catching of active fish, and the elasticity resides solely in the hinges; but the common Pike possesses many hinged teeth which seem to be more concerned in the swallowing of the prey after it has been caught, and there is no elasticity in the hinges, the resilience of the teeth being provided for in another way.

The teeth which surround the margins of the jaws are anchylosed, and they are more or less solidly filled up in their interior with a development of osteo-dentine, which, by becoming continuous with the subjacent bone, cements them to it. The manner of development of this is by rods of calcifying material shooting down through the central pulp (see p. 77); in the hinged teeth also these trabeculæ shoot down, and become continuous with the subjacent bone, only instead of rigidly ossifying they remain soft and elastic, so that the tooth is like an extinguisher fastened down by a large number of elastic strings attached to different points on its interior, and hinged at one side.

Fig. 105 (1).



The elasticity is very perfect, so that the teeth depressed and suddenly released return with an audible snap; but it resides solely in these strings, for if these be divided by carefully slipping a cataract needle under the tooth without injuring the hinge, the tooth will stay in any position into which it is put.

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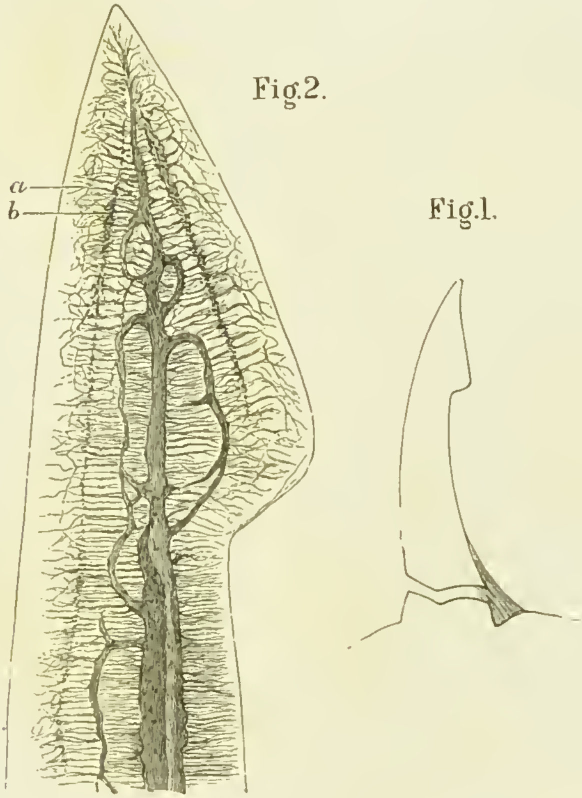
(1) Hinged tooth of Pike. *a.* Dentine. *b.* Elastic rods, formed of uncalcified trabeculæ which might have become bone. *c.* Hinge, not itself elastic. *d.* Bone of attachment. *e.* Bone of body of jaw.

Amongst the very peculiar predatory fish which were obtained by the *Challenger* from great depths, and which have been described by Dr. Günther, through whose kindness I have had the opportunity of examining them, are several which possess hinged teeth. Thus in Bathysaurus ferox, which has a crocodile-like snout, the teeth are of no very great size, but they are attached by ligamentous hinges which allow of their being bent down backwards and inwards. The teeth are not perched upon any definite pedestals, so

Fig. 106 (1).



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(1) Hinged tooth of Odontostomus, a predatory fish from great depths. *a.* Enamel penetrated by dentinal tubes. *b.* Dentine.

that the motion is not very exactly limited to one plane. But in Odontostomus hyalinus there are some more highly specialised hinged teeth, which are laterally compressed, and have a sort of barbed point which recalls the form of some primitive bone fish-hooks. The vomer carries two such teeth of great length, behind which come some smaller ones: they are perched upon little bony pedestals of such form that the attachment being made by means of an elastic ligament on one side, the motion permitted to the tooth is strictly confined to one plane.

Thus we have examples of hinged teeth occurring in several distinct orders of fish; in Acanthopterygii (Lophius), in Anacanthina (Merlucius), in Physostomi (Esox, Bathysaurus, Odontostomus), whilst on the other hand they are not universal even within the limits of well-defined families.

The points most noteworthy are, (i.) that hinged teeth have arisen independently in families of fish widely removed from one another, and (ii.) that, whilst the general object of mobility and elastic resiliency is attained in all, it is by different mechanisms, and by the least modification possible of the existing fixed teeth of the family.

Attachment by Anchylosis.—In both the socketed and the membranous manners of attachment an organised, more or less vascular, membrane intervenes between the tooth and the jaw-bone; in the method now under consideration there is no such intervening membrane, but the calcified tooth substance and the bone are in actual continuity, so that it is often difficult to discern with the naked eye the line of junction.

The teeth may be only slightly held, so that they break off under the application of only a moderate degree of force, or they may be so intimately bound to the bone that a portion of the latter will usually be torn away with the tooth.

A very perfect example of attachment by anchylosis is afforded by the fixed teeth of the Pike, of which the central core is composed of osteo-dentine. The method by which the entire fusion of this tissue with the bone beneath it takes place has already been alluded to, the similarity of its method of calcification with that of bone rendering the fusion easy and complete.

And in certain extinct fish, whose nearest ally is now the anomalous Australian shark, the Cestracion Philippi, the lower part of the tooth is composed of osteo-dentine, which so closely resembles bone itself that it is impossible to say at which point the bone may be said to commence and the tooth to end; but even where this intimate resemblance in histological character does not exist, there is often to be found more or less blending of the basal dentine with the bone beneath it, so that there is even here a sort of transitional region.

From the accounts which pass current in most text books it would be supposed that the process of attachment by anchylosis is a very simple matter, the base of the dentine papilla, or the dental capsule, by its calcification cementing the tooth on to a surface of the jaw-bone already formed. In a few animals which I have examined (1), however, I have found that this conception does not at all adequately represent what really takes place; it seldom, perhaps never, happens that a tooth is attached directly to a plane surface of the jaw which has been formed previously; but the union takes place through the medium of a portion of bone (which may be large or small in amount) which is specially developed to give attachment to that one particular tooth, and after the fall of that tooth is itself removed.

For this bone I have proposed the name of "bone of attachment," and it is well exemplified in the Ophidia, a description of the fixation of the teeth of which will serve to convey a good idea of its general character. If the base of one of the teeth, with the subjacent jaw-bone, be submitted to microscopic examination, we shall find that the layer of bone which closely embraces the tooth contrasts markedly with the rest of the bone. The latter is fine in texture, its lacunæ, with their very numerous fine canaliculi, very regular, and the lamination obviously referable to the general surface of the bone. But the "bone of attachment," is very coarse in texture, full of irregular spaces, very different from the regular lacunæ, and its lamination is roughly parallel with the base of the tooth. The dentine of the base of the tooth also bends inwards (Fig. 107), and its tubes are lost in the osseous tissue, a blending so intimate resulting, that in grinding down sections the tooth and the bone of attachment often come away together, the tooth and this bone being more intimately united than this special bone is with that of the rest of the jaw.

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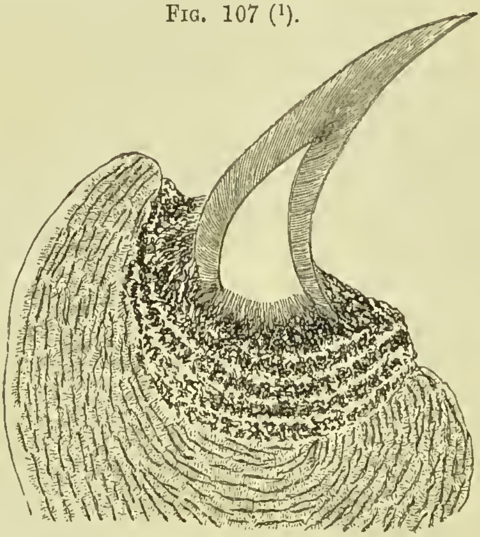
(1) "Transactions of the Odontological Society," Dec. 1874.—"Studies on the Attachment of Teeth."

FIG. 107 (1).



Its development has not been adequately studied: it has an intimate relation with the tooth with which it is continuous, for it is wholly removed with the fall of the tooth, and is specially developed again for the next tooth which comes into position. What share is taken by the periosteum of the rest of the jaw-bone in the formation of this special bone substance, and what by the tooth capsule is not known, though recently Kathariner has argued that the tissue here termed bone of attachment is really cementum.

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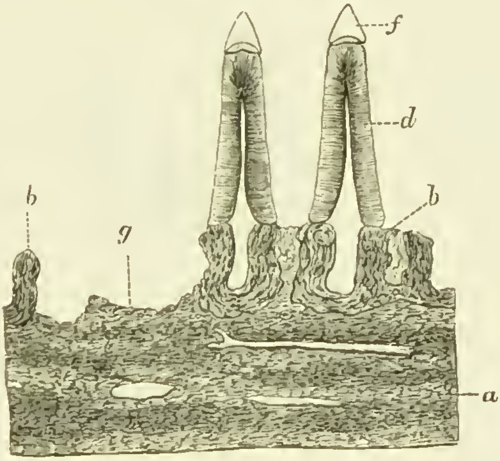
(1) Section of tooth and a portion of the jaw of a python, showing the marked difference in character between the bone of attachment and the rest of the bone.

Hertwig throws out the suggestion that parts of the tooth sockets and of the basal plates met with in fish and reptiles represent the cementum, and that it may even be that the bones surrounding the mouth may have originated from the coalescence of such plates, but this view does not commend itself to me.

In the frog the teeth are commonly described as being attached by their bases and outer surface to a continuous groove, of which the external wall is the highest. Such is, however, an inadequate description of the process, the tooth as seen in section being attached on its outer side by a new development of special bone, which extends for a short distance up over its external surface; and for the support of its inner wall there springs up from the subjacent bone a pillar of bone, which is entirely removed when that tooth falls, a new pillar being developed for the next tooth.

FIG. 108 (¹).



When the teeth are, as in many fish, implanted upon what to the naked eye appears nothing more than a plane surface of bone, a microscopic examination generally, in fact in all specimens which I have examined, reveals that the

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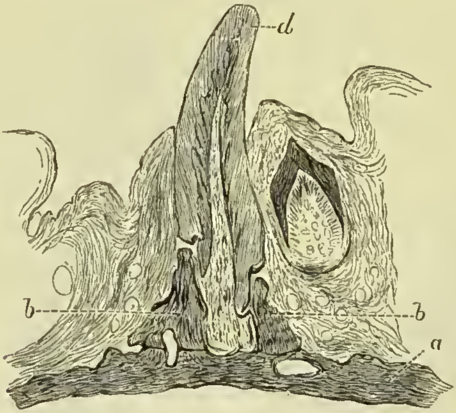
(¹) From lower jaw of an eel. *a.* Bone of jaw. *b.* Bone of attachment. *d.* Dentine. *f.* Enamel. *g.* Space vacated by a shed tooth.

individual teeth are implanted in depressions much larger than themselves, the excess of space being occupied by new and specially formed bone; or else that the teeth surmount pedicles, which are closely set together, the interspaces being occupied with a less regular calcified structure.

A good example of the latter method is afforded by the Eel (Fig. 108), in which each tooth surmounts a short hollow cylinder of bone, the lamination, &c., of which differs strongly from that of the body of the jaw-bone. When the tooth which it carries is shed, the bone of attachment, in this case a hollow cylinder, is removed right down to the level of the main bone of the jaw, as is well seen in the figure to the left of the teeth in position. Under a higher magnifying power the bone at this point would be found to be excavated by "Howship's lacunæ." As an anchylosis, the implantation of the teeth is less perfect than that of those of the snake, for the dentinal tubes at the base of the tooth are not deflected, and do not in any sense blend with the bone beneath them. Accordingly, the teeth are far less firmly attached, and break off quite readily.

Fig. 109 (1).



A transition towards the socketed type of implantation is furnished by some of the Cod family. In the haddock, for example, the teeth surmount hollow cylinders of "bone of attachment," resembling in many particulars those of the eel; the teeth do not, however, simply surmount the bony cylinders, but are continued for a short distance within them, definite shoulders being formed which rest on the rims of the cylinder. The base of the tooth does not, however, contract or taper any more, and is widely open, so that it cannot be considered that any close approximation to a root is made. The pulp cavity of the tooth becomes continuous with the cavity of the osseous cylinder, into which the pulp is for a short distance continued. Not only is the pulp continued down, but its odontoblast layer is traceable here, and this relation of parts recalls that seen in Sargus. (Cf. Fig. 91, p. 188.)

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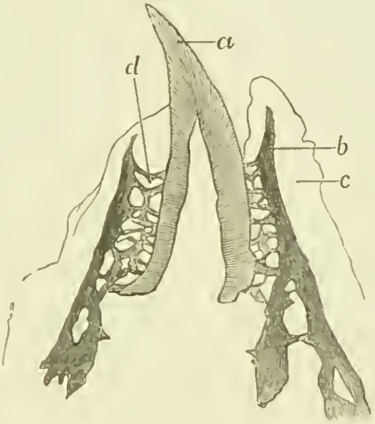
(1) From lower jaw of a haddock. *a.* Bone of jaw. *b.* Bone of attachment. *d.* Dentine of tooth.

FIG. 110 (1).



The bony supports of the teeth originate in many osseous trabeculæ which spring up simultaneously from the bone of the jaw beneath the new tooth; these coalesce to form a net-like skeleton, which rapidly becomes filled in by the progress of ossification. So far as my own researches enable me to say, there is this much in common in all forms of attachment by anchylosis, no matter how different the naked eye results of the process may be: the tooth, as it comes into position, is secured by an exceedingly rapid development of bone, which is more or less directly an outgrowth from the jaw-bone itself, which is in some unseen manner stimulated into activity by the proximity of the tooth.

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(1) Tooth of mackerel, showing its peculiar mode of anchylosis. *a.* Tooth. *b.* Bone of jaw. c. Gums and stems. *d.* Bone of attachment.

The teeth of the mackerel present an interesting variety of attachment by anchylosis. The margins of the jaws are very thin, and by no means fleshy, and in this thin margin there is a deep groove between the outer and inner plates of the bone. In this groove are the teeth, their sharp points projecting beyond the edges of the bone, and they are held in their places by a network or scaffolding of bone of attachment which is developed between their sides and the inner surface of the bone. They are, so to speak, hung up in their place, and their open bases rest on nothing, or at least on nothing hard.

Attachment by implantation in a socket.—In this, as in anchylosis, there is a special development of bone, which is modelled to the base of the tooth, but instead of its being in actual close continuity with the dental tissues, there intervenes a vascular organised membrane in great part, at all events, derived from the tooth sac. The manner in which the sockets are, so to speak, plastered around the roots of the teeth, and are perfectly subservient to and dependent on them, has already been described; little, therefore, need be added here, save that the soft tissue intervening between the bone and the tooth is not separable, either anatomically or from the point of view of development, into any two layers, but is a single membrane termed the "alveolo-dental periosteum." That it is single when it is completed, is a matter of absolute certainty; there is no difficulty in demonstrating it *in situ*, with vessels and bundles of fibres traversing its whole thickness from the tooth to the bone, or *vice versâ.*

The nature and development of the sockets in those few reptiles and fishes which have socketed teeth require further examination. I am not, from what I have seen in sections of the jaws of a young crocodile, inclined to regard them as in all respects similar to the alveoli of mammalian teeth. At all events they are not developed in that same subserviency to each individual tooth; on the contrary, successive teeth come up and occupy a socket which is more or less already in existence.

Although there are animals in which implantation in a spurious socket is supplemented by anchylosis to the wall or to the bottom of the socket, few examples of anchylosis occurring between the tooth and the bone of the socket have ever been met with in man, or indeed in any mammal, exemplifying a typical socketed implantation of the teeth.

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HEUDNER. Beitrage zur Lehre von der Knochenentwickelung, &c.
TOMES, CHARLES S. On Vascular Dentine and Hinged Teeth. Philos. Transac. 1878, and Quart. Journal Micros. Science, vol. xvii. new series.
Transac. Odontolog. Soc. 1874–1876.

CHAPTER VII.

THE TEETH OF FISHES.

In the following pages nothing more than a brief account of a few typical forms can be attempted; the limits of space forbid the mention of many creatures, or the insertion of detailed descriptions of the dentition even of the few which are included. In the class of fish the task of selection of the forms for description is no easy one; for the almost infinite diversity of dentition which exists in it makes it a matter of peculiar difficulty to frame any general account, or to do more than present before the reader a description of a few individual forms from which he may gather, as best he can, a general idea of piscine dentition.

The class of Fishes is divided into four sub-classes:—

LEPTOCARDII. Heart replaced by pulsating sinuses. Skeleton notochordal and membrano-cartilaginous. No skull, no brain.

CYCLOSTOMATA. Head without bulbus arteriosus. Skeleton cartilaginous and notochordal. No jaws; mouth surrounded by a circular lip.

TELEOSTEI. Non-contractile bulbus arteriosus. No spiral valve in intestine. Optic nerves decussating. Skeleton ossified, with completely separated vertebræ.

PALÆICHTHYES. Heart and contractile conus arteriosus; intestine with spiral valve; optic nerve non-decussating or only partially decussating.

Of Leptocardii (the single genus Amphioxus or Branchiostoma) there is nothing to be said, as it has no jaws and therefore no teeth.

The Cyclostomata comprise the lampreys and the very peculiar parasitic fish, the Myxine and Bdellostoma, which bore their way into the bodies of other fish; the cod is often attacked by the Myxine. The lampreys, which also are predatory, attaching themselves by their sucking mouth to the bodies of other fish from which they scrape off the flesh, have a round mouth, the margins of which are beset with rows of small conical teeth, there being two larger blade-shaped teeth, called from their relative position the mandibular and maxillary teeth, in the centre.

Until recently little was known of the structure of horny teeth, but they have been investigated by Dr. Beard ("Centralblatt f. Wissen. Anat." iii. 1888, nr. 6), who finds that the horny cone rests upon a slight dermal papilla, and fits into special epidermal depressions at the base of the papilla (in Pteromyzon fluviatilis); but in P. marinus there are superimposed cones "like a nest of Chinese boxes." Each of these layers arises from a separate epidermal depression, which goes on continually forming horn, so that the under cones are in no sense reserve teeth, for as each tooth is worn away at the apex fresh horny matter is formed below and pushed forwards. There is thus no resemblance to the teeth of higher vertebrates.

In a young lamprey there are to be found what at first sight look like true tooth sacs, but the dental papilla never forms any odontoblasts, and the epithelium which corresponds to the enamel organ produces horn; this is true of the marginal teeth, but further in towards the centre the teeth are formed simply in the basal layers of the epithelium, without the intervention of any sort of tooth sac.

But in the Myxine and Bdellostoma there is a very interesting and unexpected arrangement of structures. They have a large, sharply-pointed median tooth and two comb-like smaller teeth upon the tongue, and the working surface of the teeth is composed of horn similar both in structure and development to that found in the lamprey.

Dr. Beard describes the tooth of Bdellostoma as consisting of a cap of horn, which is thick and strong, and of a bright yellow colour; beneath this comes a layer of epithelium, and next to this a hard calcified material, which is to be regarded as some form of dentine. Some doubt is, however, thrown upon the nature of this calcified dentine by Prof. Howes. ("Nature," Nov. 1894.)

The horny cap is fitted into an epithelial groove at its base, so that it increases in length from the cells of this groove becoming cornified, and in thickness by a similar conversion of the epithelial layer beneath it.

The hard cone which forms, so to speak, the body of the tooth is an anomalous structure, not closely corresponding with any known form of dentine, but yet it is undoubtedly the product of an odontoblast layer upon the pulp, which latter remains in the base of the cone of dentine in the usual way.

The great hardness of the tooth and of the horny cap renders it a very difficult matter to get good sections, and hence the minute structure has not been very fully described. At the apex of the cone is a thin structureless layer, which Dr. Beard thinks may be enamel (the frequent occurrence of thin outer structureless layers upon dentine, however, would seem to render this determination open to uncertainty). There is, however, a layer of epithelium, in the proper situation, which has the characters of an enamel organ in so far as the presence of long columnar cells go.

The dentine cap appears to contain small dentinal tubes, and also vascular canals of larger size arranged with considerable regularity.

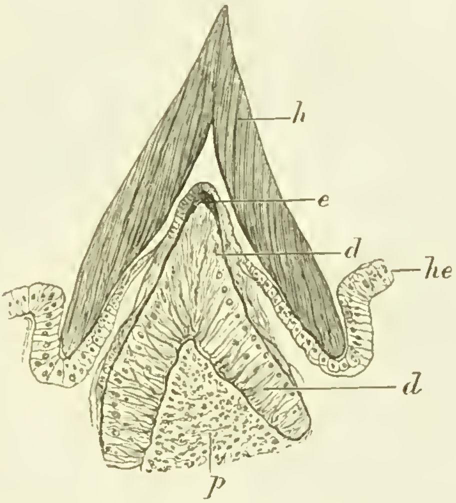
It is difficult to conceive that the presence of the calcified cap can be of much, if any, service whilst buried beneath the horny cap, and we must regard these structures not as an early and simple form of tooth, but as being degenerated teeth. And they would thus lend support to the idea, already arrived at on other grounds, that these fish had as ancestors fish which had jaws, and teeth carried upon them.

It is to be noted that the relation which the horn cone bears to the dental papilla and its dentine is entirely different from that borne by the horny teeth of Ornithorhynchus, in which the horny plate which takes the place of teeth in the adult lies beneath the teeth.

It has been suggested by Dr. Beard that the fusion of the lingual teeth of Myxine into a serrated plate may indicate the manner in which the serrated horny jaws of Chelonians may have originated, as a substitution of horny tissue for true teeth upon which they were once superimposed; and similar speculations have been indulged in as to the manner in which the bird's bill may have originated from the substitution of a number of coalescent horny teeth for true teeth, but the material for such generalisation is not yet to hand.

As in the matter of teeth the Palæichthyes, comprising the Sharks and Rays and the Ganoid fish, present somewhat simpler conditions than are met with in the osseous fish, it will be convenient to describe their teeth first, although in most respects they stand at the head of the class of fishes, and present many indications of affinity with the Batrachia.

Fig. 111 (1).



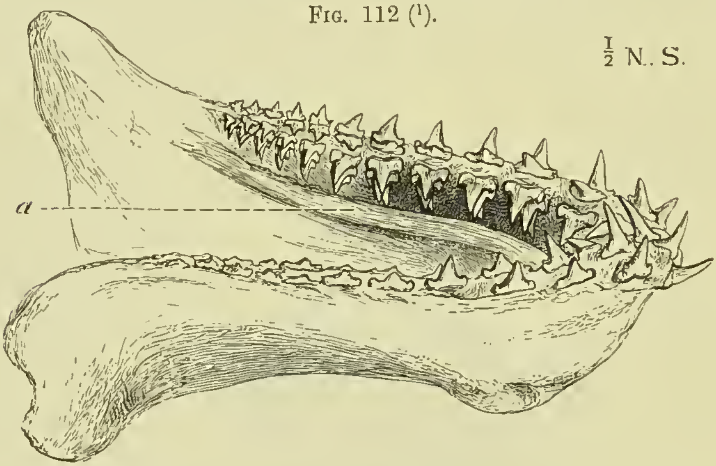
In Sharks, the scales of other fish are replaced by calcified papillæ, which have somewhat the same structure as their teeth: to these the "shagreen," as shark skin is termed, owes its roughness. The mouth is a transverse, more or less curved fissure, opening upon the under surface of the head at some little distance behind the end of the snout. Hence it is that a shark in seizing its prey turns over upon its back, or at all events upon its side.

---

(1) Tooth of Bdellostoma, Semidiagrammatic, after Dr. Beard. *d.* Calcified dentine cap. *e.* (?) Enamel. *h.* Horny tooth. *he.* Epithelial groove in which the base is formed.

The jaws, which are made up of the representatives of the palato-quadrate arch, and of Meckel's cartilage, neither true maxillæ nor premaxillæ being present, are cartilaginous in the main (although covered with a more or less ossified crust), and therefore shrink and become much distorted in drying. The shape of the jaws differs in the various groups of Plagiostomi, in some each of the two jaws being a tolerably perfect semicircle, while in others they are nearly straight and parallel to one another (see Fig. 112 and Fig. 116); but in all the rounded working surface of the jaw is clothed or encased by teeth, which are arranged in many parallel concentric rows.

FIG. 112 (1).



The teeth which are situated upon the edge or exposed border of the jaw, are usually erect, whilst the rows which lie behind them, farther within the mouth, point backwards, and are more or less recumbent, not having yet come into full use.

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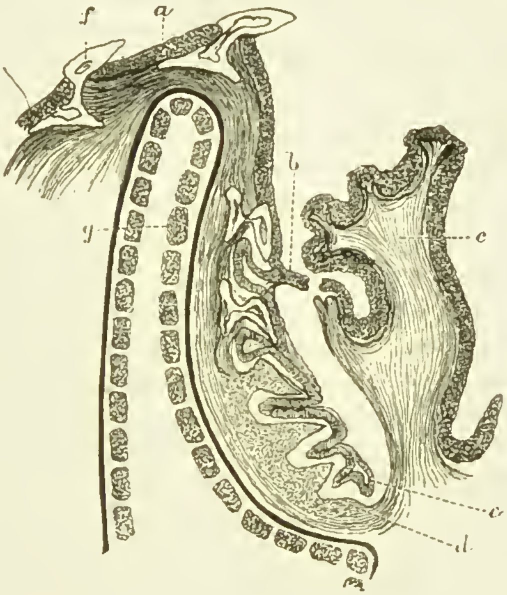
(1) Lower jaw of Lamna. *a*, Edge of flap of mucous membrane which covers the teeth not yet completed.

In this respect, however, marked difference exists among various genera of sharks; for instance, in the great tropical white shark the teeth which lie on the border of the jaw are erect, and all the successive rows are quite recumbent; whereas in many of the dog-fishes the inner surface of the jaws forms an even rounded surface along which the rows of teeth are disposed in every intermediate position between those fully recumbent at the innermost part of the jaw and those fully erected upon its exposed borders. Only a few of the most forward rows of teeth are exposed, a fold or flap of mucous membrane covering in those teeth which are not as yet fully calcified and firmly attached to the gums.

In Lamna, which may be taken as fairly illustrative, the

FIG. 113 (1).



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(1) Transverse section of lower jaw of a dog-fish. *a.* Oral epithelium. *b.* Oral epithelium passing on to flap. *c.* Protecting flap of mucous membrane (thecal fold). *d.* Youngest dentine pulp. *e.* Youngest enamel organ. *f.* Tooth about to be shed. *g.* Calcified crust of jaw.

teeth are arranged round the jaws in concentric rows with great regularity, the teeth of the successive rows corresponding in position to the teeth of older rows, and not, as is the case in some other sharks, to their interspaces. They are attached by being embedded in a densely fibrous gum, which closely embraces their bifurcated bases; and this dense gum, carrying with it the teeth, slides bodily upwards over the inner face of the jaw, and outwards over its border, beyond which it, to borrow a phrase from geological science, has an "outcrop."

In Lamna the second and third rows of teeth are only partially erect, the rows behind these lying recumbent, and being in the fresh state covered in by the fold of mucous membrane, which, being dried and shrunk in the specimen figured, falls far short of its original level.

Thus rows of teeth originally developed at the base of the jaw are carried upwards, come to occupy the foremost position on the border of the jaw, and are cast off when they pass the point *f* in the figure. It is thus easy to understand why sharks' teeth are so abundantly found in a fossil condition, although other indications of the existence of the fish are rare enough; for every shark in the course of its life casts off great numbers of teeth, which fall to the bottom of the sea and become bedded in the deposit there forming.

The teeth are never anchylosed to the jaw, nor have they any direct connection with it, but, as before mentioned, are retained by being bedded in a very tough fibrous membrane; the nature of their fixation has been more exactly described at another page (p. 222).

The sheet of fibrous gum slides bodily over the curved surface of the jaw, continually bringing up from below fresh rows of teeth, as was proved by André's specimen; and it may be worth while to condense from Professor Owen the description of the manner in which it was thus proved that an actual sliding or rotation of the membrane does really take place, and that the whole bony jaw itself does not become slowly everted. The spine of a sting ray had been driven through the lower jaw of a shark (Galeus), passing between two (vertical) rows of teeth which had not yet been brought into use; when the specimen came under observation the spine had remained in this situation, transfixing the jaw, for a long time, as was evidenced by all the teeth of these two rows, both above and below it, being stunted and smaller than their neighbours.

Hence the development of these teeth, which ultimately came to be at some little distance from the spine, had been profoundly modified by its presence, and it is difficult to understand in what manner this could have affected them had they not, at an earlier period of their growth, lain in more immediate proximity to it. But if the membrane, with the teeth attached, did move slowly along the surface of the jaw, this difficulty at once disappears.

The forms of the teeth in various sharks are different and characteristic; nevertheless they vary somewhat with age in some species, and present differences in size and form in the upper and lower jaws, or in different parts of the mouth of the same individual. For instance, in Lamna, in the upper jaw, the teeth of the third vertical row, counting from the middle line, are very small, while in both jaws there is a gradual diminution in the size of the teeth towards the back of the mouth.

Thus, although it is often possible to refer a particular tooth to its right genus or even species, much care is requisite in so doing.

The teeth of the bloodthirsty white shark (Carcharias) are triangular flattened plates, rounded on their posterior aspect, with trenchant slightly serrated edges; it is pointed out by Professor Owen that if the relation between the size of the teeth and that of the body were the same in extinct as in recent sharks, the dimensions of the teeth of the tertiary Carcharodon would indicate the existence of sharks as large as whales.

The intimate relationship between the teeth and the dermal spines, which from the standpoint of development, has been illustrated at p. 3 and pp. 112 and 145, is apparent also in their histological structure. There are many dermal spines to be met with in the sharks, and on the back or tail of rays, which seen alone could not possibly be distinguished from teeth, the resemblance both in outer form, in minute structure, and manner of development being most complete. The tooth figured on p. 79 is a fair example of a structure very common among the sharks, viz., a central body of osteo-dentine, the outer portion of which is covered by an enamel (?) of peculiar structure. Fine tubed dentine is, however, also frequently met with, as is the case of the genus Carcharias.

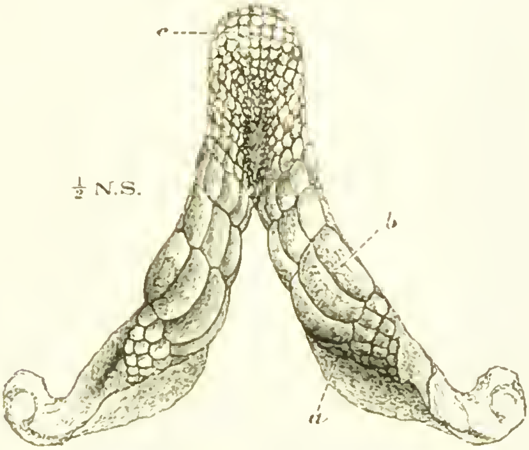
Dental tissues occur in other parts of the mouths of Selachia than upon the jaws, not only in the embryonic stages, but in the adult. Thus Professor Sir W. Turner has described ("Proc. Roy. Society, Edinburgh," 1880), very numerous comb-like appendages 5 inches long upon the branchial arches of the Basking Shark (Selache maxima), which apparently perform the same function as whalebone in straining the water. These combs are formed of a variety of dentine (? osteo-dentine), and closely resemble in structure the true teeth, which are, however, very small in this shark.

In the seas of Australia there exists a shark, the Cestracion Philippi, with a very aberrant dentition to which great interest attaches, inasmuch as it is the sole surviving representative of forms once spread all over the world. In the front of the mouth the teeth are small and very numerous; they are flat plates fitted by their edges to one another, while from their centres spring up sharp points, soon worn off when the tooth reaches such a position upon the jaw that it comes into use.

Proceeding backwards, the teeth cease to be pointed, increase in size, and become fewer in each row; a reference to the figure will convey a better idea of their general form than any description. Those which have come into use are, towards the back of the mouth, always much worn; their shedding and renewal takes place, as in other sharks, by a rotation of the mucous membrane over the surface of the jaw, so that, as might have been expected, large numbers of the isolated fossil teeth of Cestracionts are to be met with.

The teeth of the Cestracion are fitted for the trituration of hard substances, and for such they are used, its food consisting of shell-fish, &c. The teeth consist of a body of dentine partaking of the character of osteo- rather than of vaso-dentine, whilst the surface layer is made up of sharply-defined layers of fine parallel tubes, curiously gathered into bundles, which taper both towards the surface and towards the deeper part of the tooth. A comparison with other Selachian teeth indicates that this layer may be regarded as a curiously modified enamel (p. 35).

FIG. 114 (1).



The extinct Cestracionts extended far back in time, being met with in palæozoic strata, and they were equally widely distributed in space; the size of many of the teeth also indicates the existence of forms much larger than the recent timid and inoffensive Cestracion Philippi. Many of the extinct forms are known only by isolated teeth; of others, portions of the jaw with teeth *in situ* have been discovered; thus fragments of the jaw of Acrodus, the isolated fossil teeth of which have been compared to fossil leeches, with seven teeth arranged in series, have been met with.

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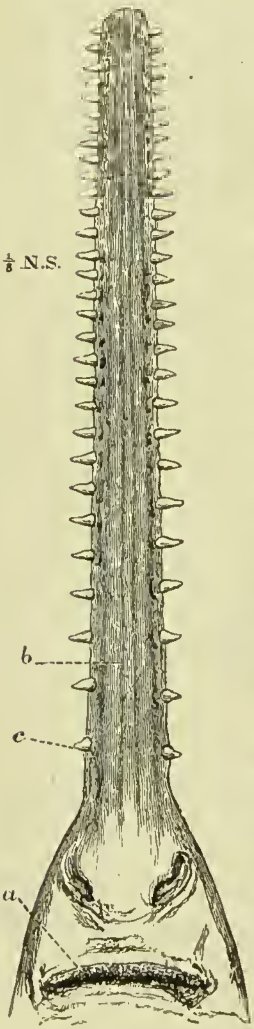
(1) Lower jaw of Cestracion Philippi. *a.* Young teeth not yet in use. *b.* Large grinding back teeth. *c.* Small pointed front teeth.

The new teeth are developed at the bottom of the series on the inner side, and, just as in other sharks, are covered in by a flap of mucous membrane.

Fig. 115 ([1]).



The Pristis, or Saw-fish, so far as the mouth is concerned, is in no way remarkable, its teeth being small and blunt, like those of many rays. The snout is, however, prolonged to an enormous length, and is shaped like a gigantic spatula, its thin edges being beset by dermal spines of large size, arranged at regular intervals, and implanted in distinct sockets. These dermal spines, or rostral teeth, as they are sometimes termed, are not shed and replaced, but grow from persistent pulps; in structure they somewhat closely resemble the teeth of Myliobates (see p. 67), being made up of parallel denticles, in the centre of each of which is a pulp cavity or medullary canal.

What use the Saw-fish makes of its armed snout is not very certainly known, but its rostral teeth are of interest to the odontologist for several reasons—the one that they are dermal spines, having a structure all but identical with that of the actual teeth of another ray, the Myliobates, while the scales of Pristis have a structure such that it is easy to imagine that these large spines are an aggregation of a number of the ordinary scales, enlarged and fused together. The other is that they are socketed, a manner of implantation not at all common amongst the teeth of fishes; and yet another is that they grow from persistent pulps, also unusual in fishes.

---

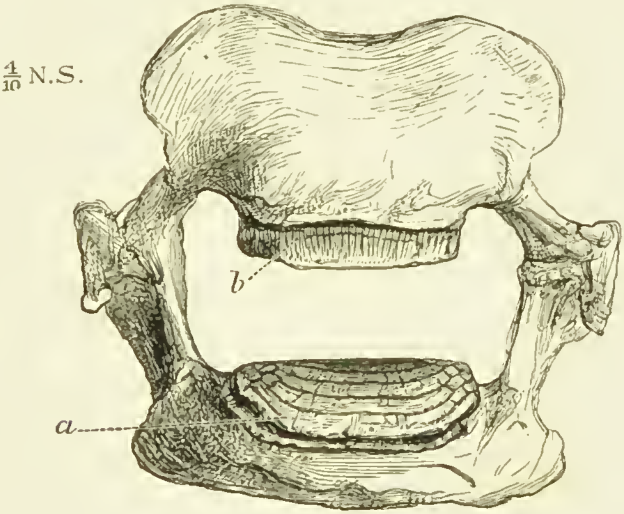
[1] Rostrum and under side of the head of a small pristis. *a*. Mouth. *b*. Rostrum. *c*. One of the rostral teeth.

The teeth, with which the margins of the jaw are covered, are so small that they cannot be represented in this figure.

Broadly speaking, the teeth of the Rays (skates) differ from those of typical sharks by being individually blunter, and being more closely set, so that they form something approaching to a continuous pavement over the jaws, with but little interspace left between the teeth.

The dentigerous surface of the jaw is very much rounded, and in some is completely encased under a pavement of teeth. Thus, in Myliobates, the powerful jaws are straight from side to side, while their working surfaces from back to front are segments of a circle. The teeth form a thick and strong pavement over the jaws, in the manner of their formation and renewal conforming with the teeth of other

FIG. 116 (¹).



(¹) Upper and lower jaw of Myliobates. At *a*, the mosaic pavement formed by the broad flattened plates which constitute its teeth is seen, these being the oldest teeth which are about to be shed off in consequence of the rotation of the whole sheet of mucous membrane over the surface of the jaws. The letter *b* indicates the under surface of one of the plates, which is seen to be finely fluted on its edges.

Plagiostomi; the severe use to which they are put is indicated by the extent to which the grinding surfaces of those teeth which have come into use are worn down.

Several genera have the jaws thus covered, the number of the teeth differing; thus Myliobates has a central series of very broad, oblong teeth, to the outer sides of which are three rows of small hexagonal teeth; in Œtobatis the large oblong central plates constitute the whole armature of the jaw.

The structure of the teeth of Myliobates has already been described and figured (see p. 67).

Amongst ganoid fish great diversity of dentition exists. Thus the sturgeons have no teeth, the mouth being at the lower surface of the snout, and being protrusible as a sort of suctorial tube. In the larval stages, however, the sturgeon possessed teeth. In the allied Spatularia there are numerous very minute teeth, whilst there are numerous extinct ganoids with large blunt-pointed teeth upon the palate and mandible.

Lepidosteus, the structure of whose teeth has been described on p. 64, has a long pointed snout furnished with large sharp conical teeth.

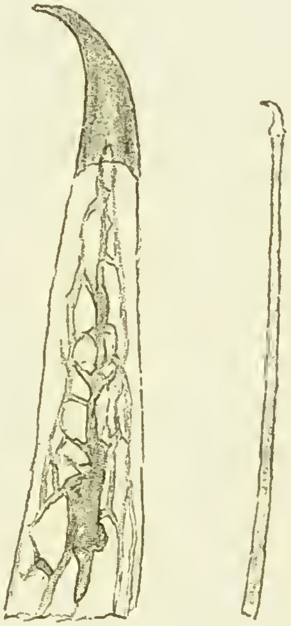
The Teleostei, or osseous fish, form the group which comprises all the fish most familiarly known to us, and within its limits the variation in dentitions is so great that few, if any, general statements can be made about them. It is not uncommon to find teeth crowded upon every one of the bones which form a part of the bony framework of the mouth and pharynx, and the teeth are sometimes in countless numbers. And such is the variability that even within the limits of single families great differences in the teeth are to be found.

The teeth of fish are of all degrees of size and of fineness; in some (Chætodonts) the teeth are as fine as hairs, and are so soft as to be flexible; they formerly were supposed to be horny, but I find that the larger ones are composed of a vascular dentine surmounted at the tip by a curious little hook of enamel.

In the finest teeth there is hardly room for vascular canals, but no one can doubt their derivation from the larger forms, so that the idea that these teeth are horny must be abandoned *in toto*.

Teeth which are very fine and very closely set are termed "dents en velours," "ciliiform" or "setiform"; when they are a little stouter, "dents en brosse," or "villiform," and when still stronger and sharper, "dents en cardes." Teeth that are conical, wedge-shaped, spheroidal, and lamelliform, are all to be met with; in fact there is infinite diversity in the form of fishes' teeth.

FIG. 117 (1).



And there are some fish, *e.g.*, some of the large Siluroids which have very strong, large teeth, an inch and a half or more long, and very firmly anchylosed to the bone.

The long and very strong snout of the Sword-fish, formed by a coalescence of maxillary and intermaxillary bones, which is able to pierce a plank, is roughened on its lower surface by villiform teeth which can be of no use, and are therefore to be regarded as rudimentary survivals.

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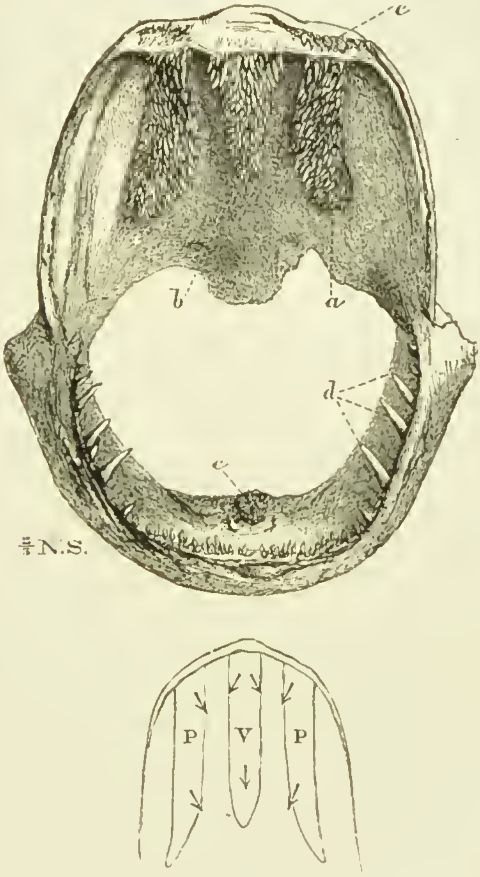
(1) Teeth of the species of Chætodon. The recurved enamel tips are apparently structureless.

In the common pike the mouth is crowded with sharply-pointed teeth, having a general inclination backwards, and being in some parts of the mouth of larger size than in others. The margin of the lower jaw is armed with teeth of formidable size and sharpness, the smallest teeth being at the front, where they are arranged in several rows, and the largest being about the middle of the side of the jaw. A pike, as is well known to anglers, when it has seized a fish often holds it across its mouth, piercing and retaining it by means of these largest teeth; then, after holding it thus for a time, and so having maimed it and lessened its power of escape, it swallows it, generally head foremost. The tenacity of the pike's hold is often illustrated when it takes a bait, and retains it so firmly that when the angler "strikes" the hooks do not get driven into the fish's mouth; but after tugging at the bait for a time the pike releases it, and the angler finds that it has never been hooked at all.

The margin of the upper jaw is not bordered by teeth, save at the front, where the intermaxillary bones carry a few teeth of insignificant dimensions; indeed, it is rather exceptional for the true maxillary bones to carry teeth in osseous fish. The roof of the mouth presents three wide parallel bands of teeth, those in the median band (on the vomer) being directed backwards, those upon the lateral bands (on the palatine bones) backwards and inwards. Some of the latter teeth are very large, but not quite so large as those at the sides of the lower jaw.

The marginal teeth are firmly anchylosed, but the teeth upon the palate are all hinged, and in such a manner that that can only bend exactly in one direction. Those of the vomerine band which lie in the middle line, will bend backwards only; those upon the outer margins of this band backwards, with an inclination outwards. Those of the lateral or palatine bands bend obliquely backwards and inwards, about at an angle of 45° with the median line of the mouth, or somewhat more directly backwards. To a body sliding over them in one direction they offer no resistance, bending down as it passes, and springing up as

Fig. 118 ([1]).



([1]) Jaws of a pike, viewed from the front, with the mouth opened more widely than is natural, so as to bring the teeth into view. *a.* Group of teeth situated on the palatine bone. *b.* Group of teeth situated on the vomer. *c.* Group of teeth situated on the lingual bone. *d.* Specially large teeth, placed at intervals round the margin of the lower jaw. *e.* Group of teeth on the intermaxillary bones.

The diagram beneath represents the direction in which the hinged teeth of the vomerine and palatine bands can bend.

the pressure is removed from them, but to anything moving in any other direction they are rigidly fixed sharp curved stakes impeding its further progress.

An elongated body of some size, such as a living fish, can only be swallowed by the pike when it is arranged lengthwise in the mouth; crosswise it cannot possibly enter the throat. The hinged teeth on the palate seem admirably arranged for getting the fish into a longitudinal position and keeping it there: for, if we imagine the fish's body held up against these teeth, and consider the direction in which the hinging of the teeth allows them to yield, it will be seen that every motion tending to arrange the body lengthwise, either in the median line of the mouth or in either of the interspaces between the vomerine and palatine bands of teeth, will meet with no obstruction, but in every deviation from this position it will be caught on the points of the teeth and resisted. Thus with the pike's mouth shut, and the fish kept up against the palatine teeth, even its own struggles will be utilised by every movement tending to place it aright being allowed, and every other stopped by the bands of hinged teeth entangling it. The structure of these teeth, and the mechanism by which they are rendered elastic, have been already described (p. 226).

The lingual bone, and the three median bones behind it, carry small teeth arranged in oblong patches; the internal surfaces of the branchial bones (which support the gills) are armed with similar small teeth; while the last or fifth branchial arch (which carries no gills, the bones forming it being called inferior pharyngeal bones,) carry larger teeth. The superior pharyngeal bones (which are median portions of the four anterior branchial arches) also carry recurved teeth larger than those which line the rest of the internal surfaces of each of the branchial arches.

The pike's mouth and pharynx thus fairly bristle with teeth, all directed somewhat backwards; and any one who has been unfortunate enough to have allowed his fingers to get entangled in the mouth of a living pike will realise how small a chance its living prey has of escape, when once it has been seized.

The teeth of the pike are composed of a central body of osteo-dentine, on the outside of which is a layer in which the dentinal tubes are directed towards the surface, as in hard or unvascular dentine (see Fig. 46); while the outermost portion of all is a very dense and hard, and apparently structureless, enamel (?) film. The teeth are anchylosed to the bone, and are very frequently renewed, their successors being developed at one side of their bases.

Though the pike has rather more teeth than many other fish, it may be taken as a fair example of most osseous fishes in this respect. Space will only allow of a few of the more exceptional forms being here described.

The angler (Lophius piscatorius), another predatory fish, found on our own coasts, with an enormous mouth and disproportionately small body and tail, lies hidden in the mud, or crouched upon the bottom, and makes a rush upon smaller fishes which approach sufficiently near to it; it is remarkable for the manner of attachment of the teeth, some of the largest of which upon the edges of its jaws do not become anchylosed, but are so attached, as has been described at p. 204, as to allow of their bending in and towards the mouth, but not in the opposite or indeed any other direction. The teeth of the outer row are firmly anchylosed to the margins of the jaw, and the far larger hinged teeth form a sort of irregular second row.

The benefit of such an arrangement to a fish of its habit is sufficiently obvious; its teeth allow the utmost freedom of entry, but offer obstacles to anything getting out again.

This arrangement of teeth, long supposed to be unique, is closely paralleled in a very different fish, the Hake (Merlucius, one of the Gadidæ). This fish, the most active and predatory of the Cod family, follows shoals of pilchards and of herrings, themselves active fish, and feeds upon them. The margins of the jaws carry two distinct and regularly arranged rows of teeth, an outer smaller row which are anchylosed, and an inner longer row which are hinged.

They are very sharp, being tipped with spear points of enamel, and are recurved. In the fresh state they look quite red, being composed of a richly vascular vaso-dentine.

The family of Codfishes (Gadidæ) present an interesting series of gradations between teeth immoveably fixed, teeth admitting of slight motion, and highly specialised hinged teeth, such as those of the Hake. They present also great variability in the structure of their teeth. Thus we have the rich and regular disposition of vascular canals in the Ling and Hake, the less abundant system of canals in the Cod, whilst in the Rock Cod (Motella) the dentine is laminated and contains few canals, and in Lotella, a fish found in Japan, and allied to the Hake, there are no vascular canals and no dentinal tubes, but a strongly-marked lamination is seen.

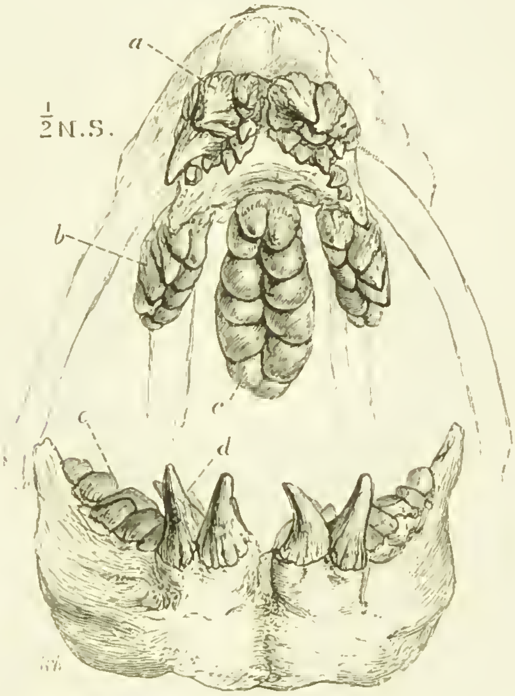
Again, in several of the deep sea fish dredged by the *Challenger* from the depths to which light does not penetrate, hinged teeth have been found (cf. p. 227). Many of these deep sea fish have very formidable dental armaments, and curiously enough, one of these, which has exceptionally long upper teeth, has a downward projection from the lower jaw, which serves to protect them while closed, an arrangement elsewhere only met with in extinct mammalia, such as Dinoceras and Machairodus figured later on in this work.

Another curious dentition is possessed by the Wolf-fish (Anarrhicas lupus), also an inhabitant of British waters, and sometimes to be seen in London fishmongers' shops under the name of the sea cat. The intermaxillary teeth are conical, bluntly pointed, and set forwards and outwards; these are antagonised by somewhat similar teeth in the front of the lower jaw. The palatine bones carry short, bluntly conical, or round-topped crushing teeth in a double row: the vomer is also armed with a double row of very much larger and shorter teeth; the lower jaw, with the exception of its anterior part, is occupied by teeth of similar character.

All the teeth of the Wolf-fish are anchylosed slightly to the bone, a definite process from which forms a sort of short pedestal for each tooth. The jaws are worked by muscles of great power, and it seldom happens that a specimen is examined in which some of the teeth are not broken. I feeds upon shell-fish, the hard coverings of which are crushed by the blunter teeth, while the pointed front teeth apparently serve to tear the shell-fish from the rocks to which they are commonly attached.

In the group of fish known as "Gymnodonts" (naked toothed), the teeth and the margins of the dentigerous bones form a sort of beak, which is not covered by the lips. The example figured on p. 256 consists of the upper and lower jaws of the Diodon, so called because it appears to casual observers to have but two teeth. A kindred fish in which the division of each jaw in the middle line is conspicuous, is similarly

Fig. 119 (1).



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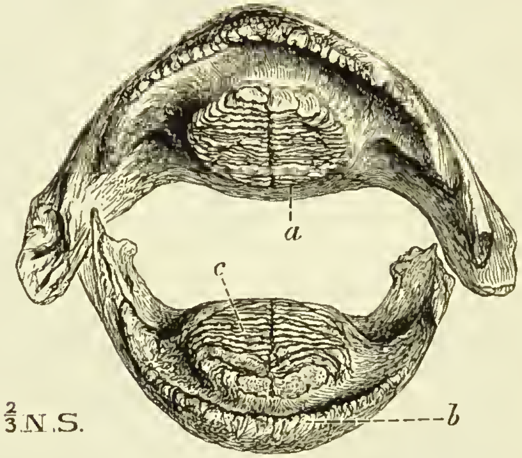
(1) Bones of the mouth of the wolf-fish (Anarrhicas lupus). The letter *a* indicates the divergent pointed teeth which occupy the intermaxillary bone; the letter *d* indicates the similar teeth which are attached to the front of the mandible, on the middle and back parts of which are round-topped crushing teeth (*e*). Strong crushing teeth are found also upon the palatine bones (*b*), and upon the vomer (*c*).

called Tetrodon. The jaw consists of teeth and bone very intimately fused together; the broad rounded mass (*c* in the figure), which lies just inside the margin of the jaw, is made up of a number of horizontal plates of dentine, the edges of which crop out upon its posterior surface; and these are united to one another by the calcification of the last remains of the pulp of each plate into a sort of osteodentine, the different hardness of the two tissues keeping the surface constantly rough, as the plates become worn away. The whole margin of the jaw is similarly built up of smaller horizontally disposed denticles, or plates of dentine, which are, as they wear down, replaced by the development of fresh plates, which are added from beneath, where they are developed in cavities situated low down in the substance of the bone.

Fig. 120 (1).



The new teeth or plates of dentine thus formed at the base of the hemispherical masses within the jaws (at the point *a*), or low down in the substance of the jaw, do not come into use by the ordinary process of displacing their predecessors, and being in turn themselves replaced, but fresh plates only come into use by the actual wearing away of all that is above them, both dentine and bone, so that they come to form the topmost portion of the jaw. The margins of the jaw are, however, mainly built up of dental tissues, there being but little bone in their interspaces.

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(1) Jaws of the Diodon. *a*. Base of the dental plates, where new lamellæ of dentine are being developed. *b*. Margin of jaw, formed mainly by the sides of the denticles. *c*. Compound tooth, made up of the superimposed lamellæ of dentine anchylosed together.

Tetrodon has not the rounded triturating disk of the Diodon, or has it but feebly represented; and the margins of the jaws are sharper.

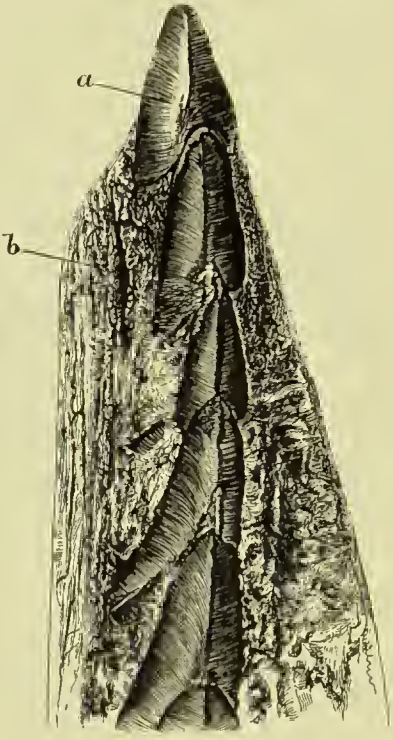
In the parrot-fishes (Scarus), which are very nearly allied to the Gymnodonts, somewhat similar beaks are found, the individual teeth being more conspicuous. The whole outer surface of the jaw near to its working edge is covered by a sort of tesselated pavement, formed by the several teeth which are pressed together into a mass, but they form only the outer surface and the immediate edge, so that the soft bone forms a part of the working surface, or would do so but that, by its more speedy wear, it leaves the edge, formed by dentine and enamel, always prominent and more or less sharp.

The structure and succession of these teeth have been carefully described by J. von Boas ("Zeits. f. Wissen. Zool." xxxii.), and the differences between the several genera pointed out. He describes cementum as binding the denticles together and forming a part of the working edge, but that which he describes as cementum appears to me to be that tissue which I have termed "bone of attachment." (See p. 229.)

In a section of a jaw in my possession, which I believed to have belonged to a Gymnodont fish but which bears a remarkably close resemblance to that figured by von Boas as being a jaw of Pseudoscarus, a very beautiful arrangement serves to preserve the sharpness of the edge of the jaw.

The denticles are conical, and form a series of hollow superimposed cones with the points upwards; they consist of dentine and enamel, and the point of the subjacent cone fits up into the hollow of that above it so closely that in von Boas' specimen the dentine of the older tooth is in great part absorbed to make way for the point of its successor; so that the working denticle comes to be little more than a hollow cone of enamel. This is not the case in my specimen, in which there is a quantity of dentine left in each denticle. This vertical series of superimposed sharp cones lie in the midst of the somewhat thin jaw-bone, fused together by cementum (? bone of attachment), and enclosed between the inner and outer plates of the jaw.

Fig. 121 (1).



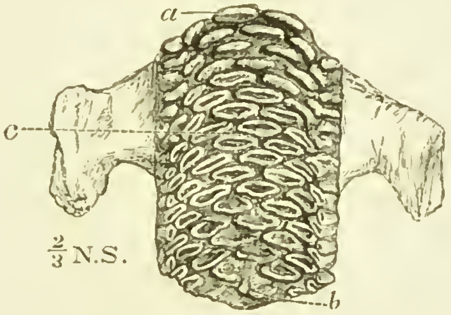
The bone being much softer than the dentine wears down much faster, so that the edge is always formed by a prominent sharp tooth, which, as the wearing down of the bone progresses, falls off, and the next one beneath it comes into play. The arrangement recalls the way in which a scythe or a chisel is assisted in keeping its edge by being

(1) Edge of jaw of Pseudoscarus (?). *a.* Denticles. *b.* Bone of jaw.

made of a plate of steel welded between two plates of softer iron.

The pharyngeal bones are also remarkable; the two lower are united into one, and the stout bone so formed is armed with teeth; it is antagonised by two upper pharyngeal bones similarly armed. It carries teeth which are anchylosed to it, and which are so disposed as to keep the surface constantly rough. When they are freshly formed the teeth have flattened thin edges, something like human incisors. The teeth are coated with enamel, and thus, when calcification has proceeded so far as to obliterate their central pulp cavities, after the tooth is worn to a certain point (*c* in Fig. 122) it presents a ring of enamel, inside which comes a ring of dentine, and inside this a core of secondary dentine, as seen in the figure. Owing to the different hardness of the three tissues a constant roughness of surface is maintained. The upper pharyngeals are similarly armed; and as the teeth and the supporting bone wear away, fresh teeth are developed at the front, so that the whole bone undergoes a sort of gliding motion backwards, the armature of the lower pharyngeal being renewed in a similar manner, save that new teeth and bone are developed at its posterior instead of its anterior extremities.

Fig. 122 (¹).



(¹) Lower pharyngeal bone of Pseudoscarus. *a*. Posterior border, at which the teeth are unworn. *c*. Oval areas formed by teeth, the points of which are worn off. *b*. Anterior edge of bone, at which the teeth are almost completely worn away.

The teeth are developed in bony crypts, below the youngest functional teeth, and perforations in the roofs of the crypts give passage to the connecting band between the tooth sac and the mucous membrane.

The Sheep's-head fish (Sargus), to which attention has been drawn on account of the peculiarities of structure which it well exemplifies, has curiously human-like incisors in the front of the mouth, and round-topped crushing teeth inside.

No more fitting place will occur for noticing the stout pharyngeal teeth which are met with in so many fish. Some fish, which are edentulous so far as the mouth proper is concerned, have the pharyngeal bones armed with teeth; in the carp and its allies, edentulous so far as the mouth proper is concerned, the two lower pharyngeal bones carry long pointed teeth, which partly oppose one another, and partly oppose a sort of horny tubercle, which is supported on a process of the base of the occipital bone.

A few fish are quite without teeth; the sturgeon, whose mouth forms a protrusible sucker, is edentulous, as are also the pipe fish, and the little sea-horse (Hippocampus), now so common in aquaria; these are to be regarded as degenerations from ancestors who possessed teeth, and not as fish who have never from the earliest times acquired teeth.

But as a rule fish are remarkable for the great number of their teeth, which are being constantly shed off and replaced by successors an indefinite number of times.

In all the fish hitherto mentioned in these pages, it happens that the teeth in different parts of the mouth differ in size and in the function which they have to perform, but this is only so because a few striking forms have been naturally selected for description. It is far commoner for all the teeth of a fish, particularly of those fish which have countless numbers of teeth, to be very nearly alike in form and size in all parts of the mouth. As a general rule, fish do not comminute their food very fully, but make use of their teeth simply for the prehension of prey, not submitting the food to any mastication whatever; their teeth are hence often mere sharp cones, slightly recurved, or set looking backwards. Thus, though the mouth of the common pike is beset with an immense number of sharp teeth, its food is swallowed whole, and very often is alive when it reaches the stomach, the sole purpose served by the teeth being the prevention of its escape when once it has been seized.

Implantation of the teeth in sockets is not usual in the class of fish, but it does occur; for example the Barracuda pike (Sphyræna) has its lancet-shaped teeth implanted in distinct sockets, to the walls of which they are said to become slightly anchylosed; the file-fish and others might also be cited. And although the succession of teeth is usually from the side, in some cases the successional teeth are developed in alveolar cavities within the substance of the bone, and displace their predecessors in a vertical direction, as happens in the pharyngeal teeth of the Wrasses, or the incisors of the Sheep's-head fish (Sargus); the Lepidosteus also has its teeth affixed in incomplete sockets, to the walls and bases of which they are anchylosed; this is not a very uncommon arrangement with the teeth of the fish when they are socketed at all.

It is not common for sexual differences to be met with between the teeth of the male and female, though a slight difference exists between the sexes in some species of Skate. And although not strictly speaking a dental character, it may not be out of place to mention here the peculiar armature of the jaw of the male Salmon at the breeding season.

The end of the lower jaw becomes produced, and turned upwards at its point; the stout cartilaginous hook thus formed is of such dimensions that it has to be accommodated during closure of the mouth in a deep cavity formed for it between the intermaxillary bones. In some Canadian salmon this process is supposed to be constant in the older males, but in the British fish it disappears, and only exists at the breeding season. After spawning it is still strongly developed, and the salmon is a foul fish and is called a Kelt. It is used apparently as a battering ram, and salmon are constantly found killed, with their sides deeply gashed by the charges of their opponents.

Not much can be said in general terms of the structure of the teeth of fish. The bulk of the teeth of most fishes is made up of one or other modification of vaso-dentine or osteo-dentine; this is often glazed over upon its exterior by a thin film of enamel, so thin as often to appear structureless.

Unvascular dentine also forms the teeth of many fish, and in some is remarkable for the fineness of its tubes; in fact, every form of dentine, from fine-tubed hard dentine to tissue indistinguishable from coarse bone, is to be found in this class.

Dentine of very complex structure (labyrintho-dentine) is met with in some fish; and an example from the Lepidosteus (American garpike, a ganoid fish) has been figured at p. 64.

Enamel is often present in a very thin layer, glazing the exterior of the dentine; sometimes it forms a mere tip, a sort of spear-point to the tooth, as in the Eel and the Hake and in Chætodonts (see Figs. 108 and 117), and sometimes it is very thick, and itself permeated by systems of tubes. (See Fig. 16.)

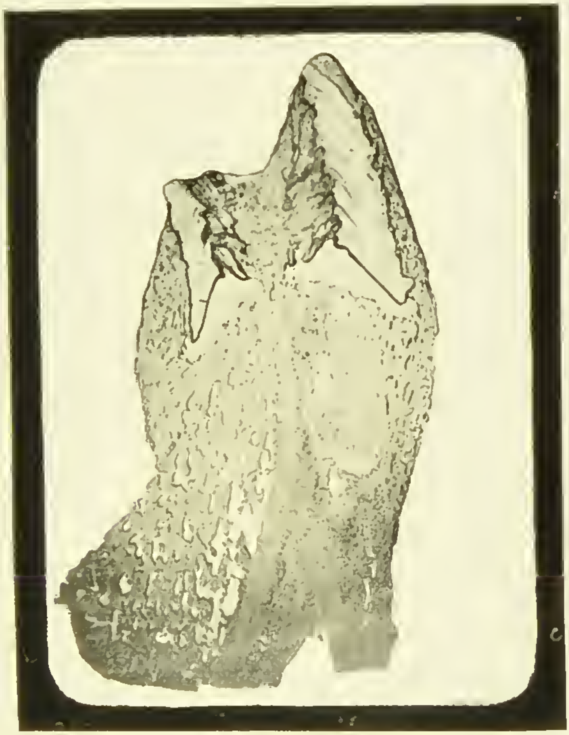
Cementum is of comparatively rare occurrence in fish.

Professor Kölliker has shown that in a very large number of fishes the skeleton more nearly resembles dentine than true bone in its structure. This is especially the case upon its surface, the jaw of the Wrasse, for instance, presenting a fine-tubed layer with no lacunæ or other irregular spaces; whilst the dermal scales and protective spines of fish are made up of a tissue much resembling dentine. (Cf. Professor Williamson, "Philos. Trans." 1849.) We may say, then, that just as in the external skin bony or dentinal plates are developed for the purpose of protecting it from destruction by attrition, so for a similar purpose teeth are developed in that portion of the mucous membrane which covers the jaws.

Near the borderland between fish and amphibia is the Lepidosiren, or Mud-fish, which is a fish rather than an amphibian. The armature of its mouth is peculiar, the margins of the lower jaws being formed by dental plates anchylosed in the bone. These plates have upon their edges five deep angular notches, the prominences of the upper plate corresponding to the notches of the lower; and the edge is kept somewhat sharp by the disposition of the hard tissues.

In the edge of the bone lie superimposed layers of a tissue which appears to be enamel, and a blunt edge is kept up by these resisting wear longer than the bone in which they are imbedded. My attention was called to this structure by Mr. Leon Williams, and I am not acquainted with any published description of it.

FIG. 123 ([1]).



A somewhat similar condition exists in Phyllodus, an extinct fish from the London clay, known only by its teeth. In this there are superimposed layers of dentine and enamel, not imbedded in bone. The dentine is, however, in small proportion, and a still further reduction in the dentine would bring it very much to the condition of the enamel plates of Lepidosiren, so that this explains the apparent anomaly of successive plates of enamel developed without dentine.

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[1] Edge of jaw of Lepidosiren, in which are developed superimposed plates of enamel. Prepared and photographed by Mr. Leon Williams.

The cutting plates of the upper jaw are developed in the median line of the palate, and there are in front of them conical piercing teeth upon that forward prolongation of the cartilage which takes the place of a distinct vomer; these have sometimes been described as being upon the nasal bone.

It would seem that the two conical piercing teeth serve as holdfasts, while the cutting edges of the deeply-notched plates are brought into play to slice up the food.

Both in structure and general disposition the dental plates in Lepidosiren are paralleled by the teeth of Ceratodus, for some time known only as a fossil, but of which recent examples have been captured near Queensland; this resemblance was suspected some years ago by my friend, the late Professor Moseley.

CHAPTER VIII.

THE TEETH OF BATRACHIA AND REPTILES.

In these classes the teeth are never so numerous nor so widely distributed upon the bones of the mouth as in fish; a double row of teeth arranged in concentric lines in the upper jaw, between which a single row of teeth upon the lower jaw passes when the mouth is closed, is an arrangement rather common amongst Batrachia. The outer of the two rows of teeth in the upper jaw is situated upon the premaxillary and maxillary bones, and usually extends further back than the vomerine or inner row. Almost all Batrachians and Reptiles have an endless succession of teeth; but there are some Lizards (*e.g.*, the Chamæleon and Hatteria, now generally known as Sphenodon) in which no replacement takes place, and none is known to take place in the Theriodonts. Only a few reptiles (*e.g.*, Hatteria, Ophisaurus, a snake-like lizard akin to the blind-worm, Chamæleon, and Dicynodon) have a row of vomerine teeth.

From this type of dentition there are many deviations; thus the toads are edentulous, and the frog has no teeth in the lower jaw.

The teeth of the frog form a single row upon the margin of the upper jaw, their points projecting but little above the surface of the mucous membrane, and the vomerine teeth are few in number and cover only a small space.

The edentulous lower jaw passes altogether inside the row of upper teeth, and having rounded surfaces and no lip, fits very closely against the inner sides of the teeth. Thus it leaves very little room for the young developing tooth sacs, which are accommodated with the space required for the attainment of their full size, by the absorption of the older solid bone and the tooth which has preceded them, in the following manner. The teeth are attached to the bone by anchylosis, each tooth being perched upon a little pedestal of bone which is specially formed for it; and the successional teeth, the germs of which originally lay at the inner sides of the old teeth, commonly undermine the sides of the pedestals and the bases of the latter, and move bodily beneath them, so that the new tooth completes its development in what was once the pulp cavity of its predecessor.

The teeth of the frog consist of a body of hard dentine, coated with an exceedingly thin layer of enamel, the existence of which has been doubted by some writers; but a study of the tooth sac of the animal renders it probable that the transparent layer which is undoubtedly there is really enamel.

The teeth of the newt and its ally the salamander are remarkable for having tips of enamel, somewhat like those of the eel (see Fig. 108), save that they are bifurcated, the one point being larger and longer than the other.

The armature of the mouth of the tadpole is peculiar and interesting. Upon its cartilaginous jaws are tough, horny plates, something in general shape like a turtle's bill; but in addition to these the inner margins of the lips are set with tiny horny spines or hooks seated upon expanded bases. Each one of these is the product of the cornification of a single epithelial cell, which has become of very large size and shaped into an extinguisher-like form. Beneath the one in use are a number of others in serial stages, ready to succeed when the top one falls off. The beaks are formed in exactly the same way, save that the cells being close side by side a continuous sheet is formed instead of isolated spines.

These horny cases are shed off prior to the commencement of true tooth formation.

Some extinct batrachia were of large size; the Labyrinthodon, the structure of whose teeth has already been described (p. 65), was furnished with a marginal row of teeth in the upper jaw, of which some few were of larger size and greater length than the others. In the lower jaw, the teeth, which are similar to those of the upper, are disposed in some sense in an incomplete double row, the series of smaller teeth not being interrupted by the occurrence of the larger tusks, but passing in unbroken series outside them. The Labyrinthodon was possessed also of palatine teeth.

The teeth were anchylosed to slight depressions or sockets, and the successional teeth were probably developed, as in the frog, at the inner side of the bases of the teeth already in position, as there are no indications of crypts within the bone.

In many reptiles teeth are developed for the merely temporary end of effecting an exit from the egg-shell. This purpose is sufficiently answered by the hard snout of the crocodiles, and by a sort of snout developed in Chelonia, but snakes and lizards have sharp teeth, which afterwards are lost, developed on the premaxillary bones; these are true teeth, formed of dentine.

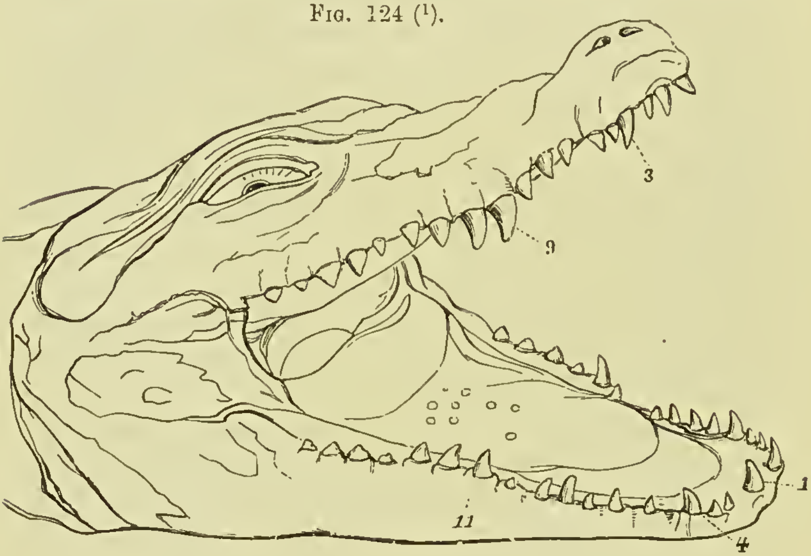
The Chelonia, comprising the Tortoises and Turtles, have no teeth, but the margins of the jaws are sheathed in horny cases, which are variously shaped in accordance with the habits of the animal, being sharp and thin-edged in carnivorous and blunt and rugged in herbivorous species.

It is stated by Röse that a tooth band exists, but that it does not go on to the formation of any definite tooth germ rudiment.

Some extinct forms of reptiles, the flying dragons (Ornithosauria), were also devoid of teeth, and had very bird-like beaks, covered presumably with horn.

It is difficult to make any very general statements as to the teeth of reptiles, as so large a variety exist. A good many, however, have simple conical teeth, either attached in grooves as in the great extinct fish lizards (Icthyosaurus), in distinct sockets as in the crocodiles, or anchylosed by their sides or by their bases to the bone as in most lizards. As a rule they are confined to the margins of the jaws, but as already mentioned, a second row of vomerine teeth sometimes exists, and, though less commonly, palatal teeth, which are flattened so as to form a sort of pavement to the roof of the mouth, are met with ; these are to be found in many extinct reptiles. In structure many of them consist of a fine-tubed dentine, with a coat of enamel, also of simple structure, but there are not wanting teeth of very complex structure, as that of the Labyrinthodon among Batrachia.

FIG. 124 (1).



The complexity of pattern arises, however, more from the existence of plicidentines than of vascular dentines, although in some, for instance the Iguanodon, there are medullary channels arranged with regularity.

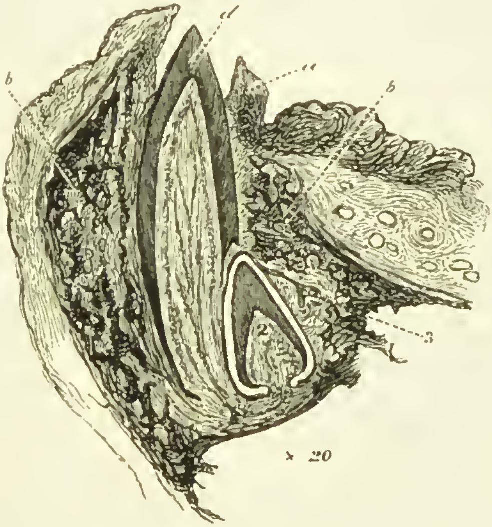
In Crocodilia the teeth are confined to the margins of the jaws, where they are very formidable in size and sharpness. The individual teeth are generally conical, sharply pointed, and often a little compressed from side to side, so as to possess sharp edges : but they vary much in form in different species.

(1) Jaws of the crocodile. The first, fourth, and eleventh teeth in the lower jaw, and the third and ninth in the upper, are seen to attain to a larger size than the others.

The teeth are lodged in distinct tubular alveolar cavities, to the walls of which they do not become anchylosed, and they are tolerably constant in number in the same species.

In parts of the mouth certain teeth are developed to a greater length than those nearest to them; thus, in the Crocodile proper, the first and fourth lower and the third and ninth upper teeth are specially large. This character is common to alligators and many crocodiles proper, the former being distinguished by the first and fourth lower teeth being received into deep pits in the upper jaw.

FIG. 125 (1).



The Garial, or slender snouted crocodile of the Ganges, has long and very narrow jaws, with slender recurved teeth, its jaws recalling those of a dolphin, like which it feeds on fish exclusively, and it is not dangerous to mammals, although the creature attains to the length of 20 feet. Various crocodiles are intermediate in respect of the length and width of their jaws between the garial and the broad-nosed alligator.

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(1) Transverse section of the lower jaw of a young alligator. *a.* Oral epithelium. *b.* Bone of socket. *d.* Dentine of old tooth. 2. Tooth next in order of succession, which is causing absorption of one side of the base of the older tooth. 3. Young tooth-germ.

In structure the teeth of crocodiles consist of hard, fine-tubed dentine, with an investing cap of enamel, and in addition a coating of cementum on their implanted portions. As already mentioned, they are implanted in tubular sockets; new successional teeth are being continually developed at the inner side of their bases, and as these attain to a certain size, absorption attacks the base of the older tooth, and its successor moves into the space so gained, so that it comes to be situated vertically beneath the older tooth. In its further growth it causes yet more absorption of the older tooth, which it ultimately pushes out in front of it, sometimes carrying the remains of the old tooth like a cap upon its own apex when it first emerges. Each new tooth vertically succeeds its predecessor; hence no additional teeth are added, but the young newly-hatched crocodile has as many teeth as a full-grown one.

In the extinct Ichthyosaurus the teeth, while forming an armature not unlike that of some of the crocodiles, were not implanted in distinct sockets, but were lodged in a continuous shallow groove, with but slight indications of transverse divisions.

The scaly reptiles, comprising the lizards and the snakes, are run somewhat into one another.

Saurians.—The lizards have teeth which are more or less conical, though in some the cone is much flattened down and rounded, the food in this very numerous group of animals varying from fruit and the like to insects, eggs, and small animals. Again, it may be complicated by serrations or vertical ridges and prominences.

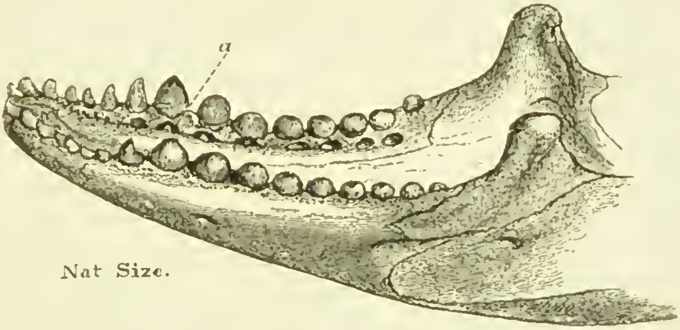
More rarely there are subsidiary cusps, generally set lengthwise, and there are but seldom inner or outer cusps which would bring it at all into the semblance of a mammalian tooth. They are generally made up of a central body of hard dentine, more or less completely invested by a cap of enamel, and they are attached to the bone by anchylosis.

When the tooth is anchylosed by its outer side to an external parapet of bone, the creature is said to be "pleurodont," when by the end of its base it is attached to the summit of a parapet it is "acrodont."

The succession of teeth in most lizards is constant, new teeth being developed at the inner side of the bases of the old teeth, which become undermined by absorption, and fall off when the successional tooth has attained to a certain stage in its development.

The accompanying figure of the lower jaw of a Monitor lizard will give an idea of a dentition common in the group. The teeth are not very large or very numerous, there being about 30 in the jaw; towards the front of the mouth they are a little more pointed than at the back, but the differences in this respect are not striking.

Fig. 126 (1).



At the inner side of the bases of the teeth are seen foramina which lead into the spaces in which new teeth are being developed.

Amongst the lizards considerable variety in the form of the teeth themselves exists, some having thin serrated edges, others being exceeding blunt and rounded, but in the general disposition of the teeth there is considerable uniformity.

The teeth of some lizards consist at their apices of ordinary hard dentine, with a simple central pulp cavity, but at their bases of plicidentine with numerous subdivisions of the pulp cavity, as is seen in the Monitor lizards (Varanus, see p. 63). One Mexican lizard (Heloderma suspectum) has the reputation of being poisonous, and has teeth which are grooved both back and front; but it is doubtful whether its harmful powers have not been exaggerated. In Heloderma the salivary glands of the lower jaw, probably the submaxillary glands, lie close against the under side of the bone. In a dissection made by Professor Stewart upon a specimen in the College of Surgeons museum, there appear to be a number of ducts which seem to actually perforate the bone, and they emerge by series of little holes which lie in the sulcus between the lip and the teeth, close to the necks of the teeth.

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(1) Lower jaw of a lizard (Varanus Gouldii). *a.* Foramina leading to cavities of reserve.

In the Python the corresponding gland also has many ducts which open in a similar position, but they attain to it without any perforation of the bone, and there is no reason to suppose that their secretion is at all poisonous; in the case of Heloderma there is, however, no doubt that the secretion is poisonous; indeed the bite of a specimen in the Zoological Gardens has been found to be fatal to small animals, and Dr. Weir Mitchell states that in one instance it has been known to be fatal to man. It is, however, of gentle disposition, and not disposed to bite.

The teeth of the Iguana are somewhat slender, and the tops are flattened, lobed, and serrated. They are pleurodont, and the successional tooth moves in sideways right into the pulp cavity of its successor.

Although most reptiles have the teeth subequal in size, in the Agamoid group of lizards it is common to find tusk-like teeth in the canine region, and molariform teeth at the back.

The Chamælcons, which differ markedly in many respects from other lizards, are peculiar in having no replacement of their teeth, though, according to Röse ("Anat. Anzeig," 1893), new teeth are constantly through life being added to the back of the series.

The absence of successional teeth is shared by another very peculiar lizard found in New Zealand, and properly known as Sphenodon, though the names Hatteria and Rhyncocephalus are still sometimes applied to it. It is a creature which is the sole survivor of a very ancient and primitive group of reptiles, and it has a very unusual dental armature. (Günther, "Phil. Trans.," 1867.) The intermaxillary bones carry two teeth, co-extensive with the bone and knife-edged, of a form which recalls the gnawing incisors of Rodents. The other teeth are all small, and there is a second inner row in the upper jaw. The great peculiarity is that the teeth are acrodont, being embedded for a short distance in the bone, to which they are intimately anchylosed.

There is no replacement of teeth at all, so that when the teeth are worn down, as happens in old specimens, the actual sharp margins of the bone come into play as masticating organs. It occurred to me as possible that these hard polished surfaces might have a coating of dentine upon them, but a microscopic examination which, by the kindness of Dr. Günther, I was enabled to make, proved that the dense ivory-like surface was true bone, and had no relation to dental structures.

With the exception of some fish, and there in a far more limited degree (cf. p. 258), there are few instances of actual bone being exposed and used for masticating purposes.

The tooth band is said to be continued beyond the germs of the functional teeth, although no successional teeth are formed.

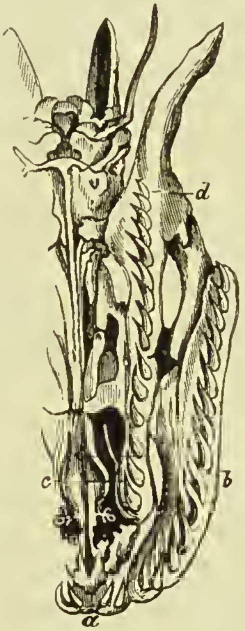
In the common blind-worm, which is zoologically a lizard which has lost its legs, the teeth are small and conical, like those of the snakes.

The OPHIDIA, or snakes, were formerly divided into two groups, the venomous and non-venomous snakes. But this division has been found to be unsatisfactory. They are, therefore, now usually grouped, with the exception of a few less important families allied to the first, into the Pythons, the Colubrine snakes, and the Viperine snakes.

The Pythons are the least specialised in their characters, and may be described first. They have one row of teeth in the lower jaw, and two rows in the upper jaw ; in the latter the maxillary bones carry one row, while a parallel internal row is supported upon the palatine and pterygoid bones.

The teeth are all strongly recurved, and are firmly anchylosed to the bone; they consist of a central body of unvascular dentine, coated by a very thin layer of enamel (there is not, as is generally supposed, any layer of cementum, the enamel having been erroneously supposed to be such).

Fig. 127 (¹).



The two halves of the lower jaw are connected at the symphysis by an exceedingly elastic ligament; their articulation with the temporal bone is through the medium of an elongated movable quadrate bone, and is also such as to allow of their being widely separated from the skull and from one another, which allows of the dilatation rendered

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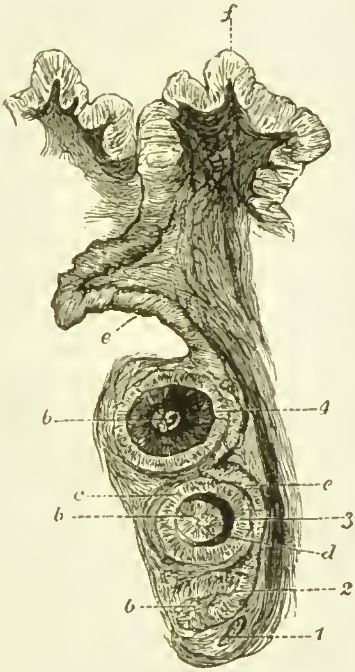
(¹) One half of the skull of a python (without the lower jaw) seen from below. *a.* Intermaxillary bone. *b.* Maxillary bone, carrying the outer row of teeth. *c. d.* Palatine bone and pterygoid bone, the teeth upon which constitute the inner or second row.

necessary by the large size of the creatures which a snake swallows.

The teeth of the snake are simply available for seizing prey and retaining it, as the snakes invariably swallow their prey whole, and in no sense masticate it.

As the object to be swallowed is often so disproportionately large as to make the process of deglutition appear an impossibility, the mouth and pharynx have to undergo great dilatation. The arrangements which combine to give to the lower jaw its mobility have just been alluded to; the successional tooth germs, which are very numerous, are also arranged in the snake in an unusual position, which by bringing them very close to the surface of the bone, to which

FIG. 128 (¹).



(¹) Developing teeth of a snake. *f.* Oral epithelium. *c.* Neck of the enamel organs. *b.* Dentine pulp. *c.* Enamel cells. *d.* Dentine. 1, 2. Very young germs. 3, 4. Older germs.

they lie parallel, renders them less liable to displacement and injury than they would have been had they been placed vertically, as they are in all other creatures; while in addition to the advantage of protection by position, they are wrapped round by a sort of adventitious capsule of connective tissue.

As the teeth during their development are thus lying down parallel with the length of the jaw-bone, when the period for their replacing a predecessor arrives, they have not only to move upwards, but also to become erected; how this is done remains a mystery, for I have been quite unable to discern the means by which it is accomplished.

When a snake has seized its food, which it retains by means of its many sharp recurved teeth, it slowly swallows it by advancing first its lower, then its upper jaw, till it thus, so to speak, forces itself over the body of its prey. When this latter is large, deglutition is a very lengthy process, but an English snake can swallow a moderate-sized frog with considerable rapidity.

It has already been mentioned that many non-venomous snakes have two complete rows of teeth in the upper jaw, the outer row being situated on the maxillary bones, the inner upon the palatine and pterygoid bones. The teeth of such snakes as the Pythons and Boas are all simple recurved cones, without grooves or canals for the conveyance of a poisonous saliva, these snakes killing their prey by crushing it in the folds of their bodies.

Whilst their dentition may be taken as typical of snakes, it is subject to reduction in some of their allies. Thus the burrowing blind snakes have few teeth, none in the lower jaw, and the mouth is not capable of that extreme dilatation characteristic of typical snakes. They eat ants and other insects and their larvæ, and the shield-tails and cylinder snakes share these peculiarities.

The Colubrine snakes form a large group, of which some are harmless and others very poisonous.

It is now usual to classify them into groups by the form of their teeth :—

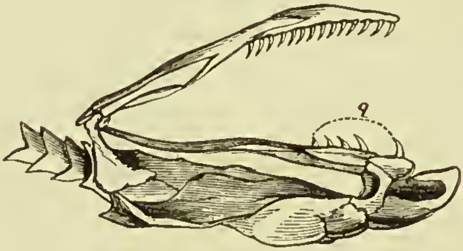
1. Aglypha. None of the maxillary teeth grooved nor canaliculated.
2. Opisthoglypha. One or more of the posterior maxillary teeth are grooved.
3. Proteroglypha. The front teeth on the maxilla are grooved or tubular.

Of the first group, or Aglypha, little need be said, as its typical members resemble in their dentition the Pythons. They are all harmless, and our common English snake is one of them. Reduced dentitions occur, as in Dasypeltis (formerly called Rachiodon), an egg-eating snake which has no teeth in front of either jaw, and but very small ones behind. Its food consists of eggs, which thus escape breakage until they reach the œsophagus, into which spinous processes from the under surface of the vertebræ project, and there serve to break the egg; snakes with their dentitions similarly modified exist also in India (*e.g.*, Elachistodon). But their jaws are dilatable to an amazing extent, so that quite a small snake will get an unbroken hen's egg down into its throat.

The Opisthoglypha are not very numerous, but the Green Tree snake and the Whip snakes belong to the group. In them the hinder grooved maxillary teeth, which are either continuous with or separated by a blank interval from the solid teeth in front, are not more than twice the length of the latter. Sometimes a lower tooth is similarly modified. They are apparently not very poisonous, and some perhaps may not be so at all.

With the Proteroglypha it is different, every one of the group being poisonous, though it may be with varying virulence. As in all the preceding snakes, the maxillary bone extends horizontally backwards and is fixed, but the front teeth upon it are more or less deeply grooved, this groove in some being so nearly closed in by its lips as to practically form a tube. The teeth which follow behind these poison fangs are usually reduced in number and solid. These poisonous snakes are characterised by a shortening of the series of teeth carried upon the maxillary bone, and by the front teeth of the series being developed to much greater length than those which lie behind it. Thus Hydrophis, a genus of poisonous sea snakes, has five or more teeth upon the maxillary bone, the foremost of which is much the largest, and this largest tooth is so deeply grooved upon its anterior surface as to be converted into a tube, the tube serving to convey the poison into the wounds inflicted by it.

Fig. 129 (1).



Enhydris has two grooved teeth, in which the groove is not closed, almost side by side at the front of each maxilla, the posterior being a little external. After an interspace five small solid teeth follow.

Hydrus has two grooved teeth, followed after an interval by seven or eight others.

Platurus has the maxilla very short and two grooved fangs, the grooves tightly closed, side by side on each maxilla. (G. S. West, "Proc. Zool. Soc.," 1895.)

Thus there is a gradation among these sea snakes leading towards the high specialisation of poison apparatus found in the Viperine group.

Although these Colubrine poisonous snakes are, so far as the elaboration of their poison apparatus goes, intermediate between the highly specialised viperine snakes and the harmless ones, it must not be supposed that they are any the less dangerous in the quality of their poison. On the contrary, some of the most virulent, such as the Cobra, are in this group, and the sea snakes just described are exceedingly deadly.

The Crait (Bungarus) is credited in India with being, next to the Cobra, the most destructive to human life. This snake has upon the maxilla from one to three solid small teeth behind the poison fang.

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(1) Head and jaws of Hydrophis. The maxillary bone (*b*), instead of carrying a complete series of teeth, is armed with a few teeth only near to the front. The foremost tooth is canaliculated, and forms the poison fang.

The Cobra has the maxilla still further shortened, it reaching back only so far as the back of the orbit, and its shortness being compensated by an increased length of the ectopterygoid ; it carries only one rudimentary tooth behind the poison fang. The front of the maxilla is wide enough to give standing space to two fangs side by side, and the inner and outer positions are, in the succession of the fangs, occupied alternately, and, although now and again two fangs will be found complete and side by side, one of them is then usually loose. The poison fang is not more than a quarter or a third of an inch long, and fits in a depression in the lower lip, while the maxilla possesses some degree of mobility, so that the tooth at rest is not fully erect, but drops down through an angle of 40°, or less. The groove on the front of the fang is closed by the approximation of its lips, but these lips remain rounded, and are not flattened out against one another to form the completely fused up joint seen in the viperine snakes. (Fig. 132.)

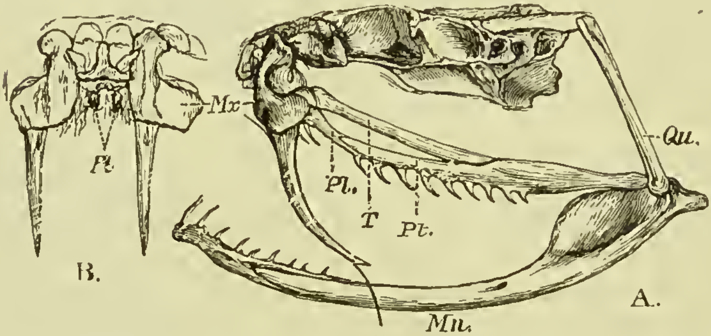
The poison in all highly specialised poisonous snakes is secreted by a very large parotid gland, the duct of which ends close to the upper orifice of the canal of the fang, but does not enter it, the escape of the poison being to a great extent prevented by a sort of flap of mucous membrane, containing, according to West, muscular elements, which embraces the front of the tooth, especially when it is somewhat elevated. But the poison ejected by an angry cobra is far larger in amount than can all pass through the canal of the fang, so that it pours down all round it as well as through it. The cobra bites like a dog, whereas the viperine snakes, though sometimes biting also, often merely strike with their much longer fangs. ("Nicholson's Indian Snakes," 1874, pp. 9—19.)

The Australian Death Adder and other poisonous snakes of that region all belong to this group.

In the Viperine poisonous snakes (Puff-Adder, Rattlesnake, Vipers, &c.) the poison apparatus is yet more specialised. The maxillary bone carries no teeth at all behind the poison fang; it is so reduced in length as to be of squarish form, and is so articulated to the skull as to be movable.

The poison fang is of great length, so that if constantly erect it would be much in the way; when it is out of use, however, it is laid flat along the roof of the mouth, and is only erected for the purpose of striking; when in repose it is altogether hidden by a fold of mucous membrane, which, when it is erected, becomes tightly stretched over a part of its anterior surface, and serves to direct the poison down the poison canal by, to a great extent, preventing its escape around the exterior of the tooth.

Fig. 130 (¹).



The mechanism by which the poison fang is erected is thus described by Professor Huxley ("Anatomy of Vertebrated Animals," p. 241):—"When the mouth is shut the axis of the quadrate bone is inclined downwards and backwards. The pterygoid, thrown back as far as it can go, straightens the pterygo-palatine joint, and causes the axis of the palatine and pterygoid bones to coincide. The transverse, also carried back by the pterygoid, similarly pulls the

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(¹) Side and front view of the skull of Bothrops (Craspedocephalus) melas, a large South American viperine snake akin to the rattlesnakes. A bristle is passed down the poison canal. *Mx.* Maxillary bones. *Mn.* Mandible. *Pl.* Palatine bones. *Pt.* Pterygoid bones. *Qu.* Quadrate bone. *T.* Transverse bone.

A. Side view. B. Front view.

posterior part of the maxilla and causes its proper palatine face, to which the great channelled poison fangs are attached, to look backwards. Hence these fangs lie along the roof of the mouth, concealed between folds of the mucous membrane. But when the animal opens its mouth for the purpose of striking its prey, the digastric muscles, pulling up the angle of the mandible, at the same time thrust the distal end of the quadrate bone forwards. This necessitates the pushing forward of the pterygoid, the result of which is twofold: firstly, the bending of the pterygo-palatine joint; secondly, the partial rotation of the maxillary upon its lachrymal joint, the hidden edge of the maxillary being thrust downwards and forwards.

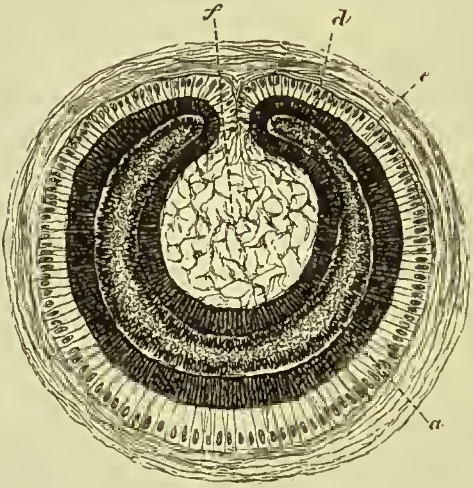
"In virtue of this rotation of the maxillary through about a quarter of a cycle, the dentigerous face of the maxilla looks downwards, and the fangs are erected into a vertical position. The snake 'strikes' by the simultaneous contraction of the crotaphite muscle, part of which extends over the poison gland, the poison is injected into the wound through the canal of the fang, and this being withdrawn, the mouth is shut, all the previous movements reversed, and the parts return to their first position."

The poison fang is a long, pointed, slightly recurved tooth, traversed by a canal which commences on its front surface, near to the bone, and terminates also on its front surface, a little distance short of its point; in the figure a bristle has been passed through it, and shows the points where it commences and terminates. This tube conveys the poison into the puncture, its upper orifice being in close relation with the end of the duct of the poison gland.

As may have been gathered from what has already been said, in colubrine poisonous snakes the canal is more or less visible on the exterior of the tooth, where an apparent fissure marks the point where the two lips of the groove have met. Thus the poison fang of Hydrophis, although in a part of its length the canal is quite closed in, has a very marked line along its front, and in section it looks much as would the dentine in Fig. 131, if the two cornua had their rounded extremities brought together into actual contact, without, however, their rounded outline being altered.

By imagining an anterior groove to be deepened, and finally converted into a canal by its edges growing up and meeting over it, we shall have a fair conception of the nature of the tube in a poison fang, which is thus really outside the tooth ; which might thus, at least in its canaliculated part, be regarded as a thin flattened tooth bent round so as to form a tube. Just as there are gradations in the armature of the maxillary bone, which link together the extreme forms of the harmless Python and the venomous Rattlesnake, so there are gradations in the form of the grooving and the completeness of the canal between the colubrine and viperine poisonous snakes.

FIG. 131 (1).



But in the poison fang of a viperine snake the lips of the groove are flattened and fitted to one another, so that not a vestige of the join can be seen upon the smooth exterior of the tooth. In the following figure the pulp cavity is seen to be a thin flattened chamber partly surrounding the tube formed for the conveyance of the poison.

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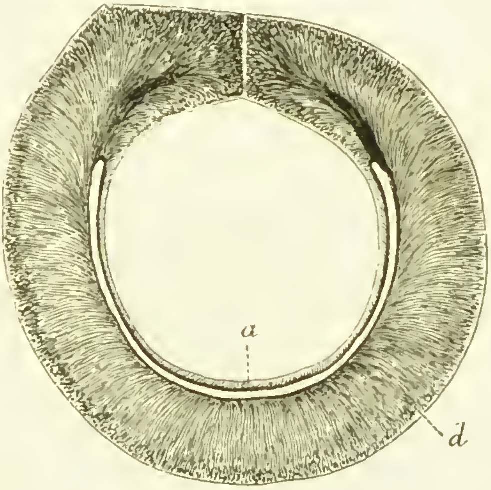
(1) Transverse section of tooth-sac of poison fang of viper, prior to the complete closure of the poison tube by the meeting together of the two cornua of the dentine.

The poison fang is exceedingly sharp, its point being continued some little distance beyond the place where the poison canal opens on the front of the tooth; this disposition of parts has been copied in the points of syringes for making subcutaneous injections.

The dentine is continued down to a very fine point, and it is cased by an exceedingly thin layer of enamel, not much more than $\frac{1}{600}$ of an inch in thickness in our common English viper: thus the utmost sharpness is secured, without loss of elasticity, which would have ensued had its point been made up of brittle enamel only. Enamel covers the whole exterior of the tooth, but does not extend into the poison canal in the viperine snakes; in Hydrophis I believe that it does. As the point is simple, the tooth germ of a poison fang only becomes distinguishable from that of another ophidian tooth after the tip of the tooth has been formed, when a groove appears in its side. (See 8 and 9 in Fig. 133.)

Fig. 132 (¹).



(¹) Transverse section of the poison fang of a rattlesnake. *a.* Pulp cavity. *d.* Dentine.

The large size of the canal in the viperine snakes enables them to send a jet of poison through it, whereas only a drop can be forced through the small canal of a cobra.

It being the habit of poisonous snakes to make use of these weapons to kill their prey, which they consequently do not swallow alive, it would obviously subject them to no little inconvenience to be without these weapons for any considerable length of time, while from their habit of striking living prey the long fangs must be very liable to being broken off by the jumping away of the creature struck, to say nothing of the great force with which the blow is given.

In the most typical (viperine) poisonous snakes the succession of teeth is conducted upon a plan which is unique, and which is excellently adapted to save loss of time in the replacement of a lost poison fang. Upon the movable maxillary bones there is space enough for two poison fangs, side by side; only one, however, is fully anchylosed to the bone at a time, and occupies a place to the extreme right or extreme left of the bone, as the case may be, leaving vacant space for another by its side.

When the tooth in use falls, it will be succeeded by a tooth upon the vacant spot by its side, not upon the spot upon which itself stood, so that the places on the right and the left of the bone are occupied alternately by the tooth in use. Thus, in Fig. 130, the poison fang of the snake's right side is seen occupying a position on the extreme outside of the maxillary bone, while its left poison fang is fixed on the inside of the maxillary bone.

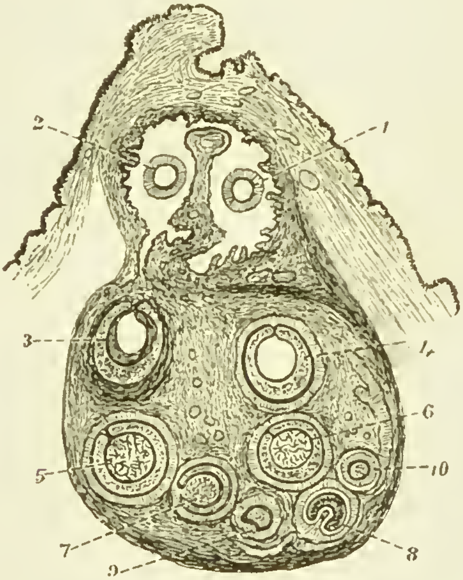
The upper boundary of Fig. 133 is formed by the flap of mucous membrane which covers in the poison fang when at rest. Nos. 1 and 2 lie in the pouch formed by it, the section happening to be taken from a specimen in which the tooth was about to be changed. In most specimens one tooth only, the tooth actually in use, is seen in this position.

A flap hanging free across this space serves apparently to keep teeth of the one series from getting over to the other side, and probably serves to hold in place the reserve tooth when the older tooth is erected for biting.

The reserve poison fangs, as many as ten in number in the Rattlesnake, are likewise arranged in two parallel series, in which the teeth exist in pairs of almost equal age; the tooth in use is thus derived alternately from the one and the other series, as is indicated by the consecutive numbers of the figure, a septum of connective tissue keeping the two series of teeth distinct from one another.

The teeth being arranged in pairs of almost equal age, suggest that the succession is both rapid and regular. All the reserve teeth lie recumbent in and behind the sheath of mucous membrane which covers in the functional tooth.

FIG. 133 (¹).



This arrangement of the successional teeth in a paired series does not exist in the Cobra, in which the successional teeth form but a single series; perhaps this may serve to explain the preference of the snake charmers for the Cobra,

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(¹) Transverse section of the reserve poison fangs of a viper. 1. Tooth at present in use, in its recumbent position; were it erect it would be withdrawn from view, or else seen in longitudinal section. 2. Tooth which will next succeed to No. 1. 3, 4, 5, &c., tooth-sacs numbered in the order in which they will succeed.

which would probably take longer to replace a removed poison fang than a viperine snake would (1).

But in the colubrine venomous snakes (cf. p. 279) the successional poison fang sometimes makes its way to a spot to the side of its predecessor, so that there may possibly be no loss of time; and notwithstanding that they are in a measure transitional forms between the harmless and the viperine snakes, some of them are most virulently poisonous and deadly in their bite (2).

This arrangement of *two* distinct chains of younger developing organs, all destined to keep the creature always supplied with *one* organ in a state of efficiency, is, so far as I know, without parallel.

A clue to the nature of the arrangement seems, however, to be afforded by some of the colubrine poisonous sea snakes (cf. p. 278), in which it was found by West that in some forms which retain more than one large tooth upon the maxilla the second tooth had moved forwards till it stood nearly or quite at the side of the first, and something of the same kind was noted in the Cobra.

It would seem, then, that the viperine snake has really retained two of its maxillary teeth, although, their development alternating, it has only one in use at a time; and that the second tooth and its chain of successors have come to be arranged in pairs with the first tooth and its successors, thus explaining an otherwise very anomalous arrangement.

Like other ophidian teeth, the poison fangs become anchylosed to the bone which carries them, their secure fixation being aided by the base of the tooth being fluted, as well as by a sort of buttress work of new bone being thrown out to secure each new poison fang as it comes into place.

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(1) An inquiry inserted in an Indian newspaper elicited the following answer :—"I have frequently seen snake-charmers exhibit snakes of the family *Viperidæ*, chiefly the Daboia Russelli and Echis carinata. I have also been told by some snake-charmers that they considered the Daboia even more poisonous than the cobra; and judging from the cautious way in which they handle these snakes—never lifting them off the ground without first putting a stick on their necks to hold them down—I feel pretty sure they all consider the vipers more dangerous than the cobras."

(2) I have given a more detailed account of the succession of poison fangs in the "Philos. Trans.," 1876, Part i.

L. Kathariner ("Zoolog. Jahrbüch Abtheil. f. Anatomie," 1897, Jena) has investigated the development of poison fangs in the viper, and holds that the two series arise from but one tooth band, a view also held by Röse. If this be true, it renders less probable the suggestion made in the text (p. 286), that the functional teeth represent not one, but really two of the once numerous maxillary teeth. However, Voerckel ("Untersuchungen, &c., der Giftzähne von Pelias," Leipzig, 1895) holds that there are two separate tooth bands, a conclusion which seems *à priori* much more probable.

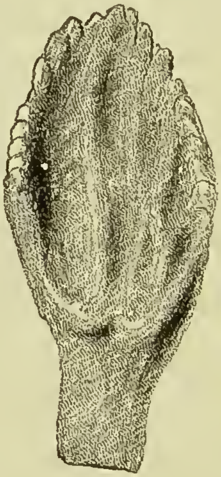
Kathariner gives a valuable description of the means by which each new tooth comes into close relation with the poison ducts, and holds, amongst other points, that the originally solid epithelial rudiment of the poison ducts sends extensions down to each series of tooth germs, and that the successional teeth travel along this opened up track to their places.

He denies the existence of enamel on these teeth, affirms that of an enamel cuticle, and states that there is not only cementum (which term he prefers to my "bone of attachment"), but also a modified dentine, which he styles fibro-dentine, intervening between the ordinary dentine and the cementum. His paper being so recent, I have been unable to re-investigate the matter since reading it.

Dinosauria.—These huge creatures flourished during the secondary period, when the mammals were but feebly represented; some of them attained a length of sixty feet or thereabouts, though there were also some small forms. They present affinities with the crocodiles and were also in some respects bird-like, the great Iguanodon, of which some fine examples are to be seen in the Brussels Museum, sitting up on their hind legs and tails, and having but short front legs. The bird-like Dinosaurs had a distinct chin bone and a contour of the front of the jaws more or less beak-shaped, and devoid of teeth in front.

The teeth were not implanted in distinct sockets, and in many of the group had an expanded and flattened crown like those of the Iguana, whence the name Iguanodon, but it must not be supposed that they therefore had any particular affinity with that lizard. In them the outer alveolar wall was considerably higher than the inner, and the transverse septa not very complete. The roots of the teeth were more or less perfectly cylindrical, and the enamelled crowns compressed and expanded, with trenchant edges. The tooth of the Iguanodon will serve as a fair example of a Dinosaurian tooth: the crown is greatly expanded, and presents anterior and posterior sharp notched margins; the enamel is laid over the outer surface of upper teeth, and the inner of lower teeth. The enamelled surface is ridged, so that as it wears down a notched edge is maintained. Moreover the maintenance of a sharp edge is further secured by the

Fig. 134 (1).



dentine on the enamelled side of the crown being of the hard unvascular variety, that on the inner being vaso-dentine and therefore softer. The remnant of the pulp ossifies, and comes into use, as these teeth remained at work until worn quite to a flat surface. The root portion was smooth, round, and curved.

Professor Marsh ("American Journal of Science," March, 1880) has described and figured a peculiar Dinosaurian dentition, in a reptile to which he gives the name of Stegosaurus; the teeth are slightly compressed transversely and are covered with a thin enamel; the roots are long and slender, implanted weakly in separate sockets. But

(1) Tooth of Iguanodon. (After Owen.)

at the inner side of the root of the tooth in use were no less than five successional teeth, in graduated stages of development, ready to ultimately take its place; so large a number of successional teeth has not hitherto been met with in a Dinosaur.

Anomodont Reptiles.—This reptilian order, established many years ago by the late Sir Richard Owen, contains a considerable number of forms which, so far as their teeth are concerned, are somewhat divergent, the order being formed upon various characters of the skull and skeleton.

The original fossils came from South Africa, whence a large number have since been obtained, but others have been found in Europe and America, also in deposits of the Triassic and Permian periods.

They have been worked at by the late Professor Huxley, Professor Cope, and others, but the most complete account is to be found in a series of elaborate papers by Professor Seeley, published in the "Philos. Trans.," 1888—1895.

By the last-named writer they are divided into two sub-orders, the Therochelonia and the Therosuchia, each of which is of the greatest interest to the odontologist, the first because it presents such a highly aberrant dentition, and the second because of the close general resemblance which the teeth present to those of mammals in some members of the group.

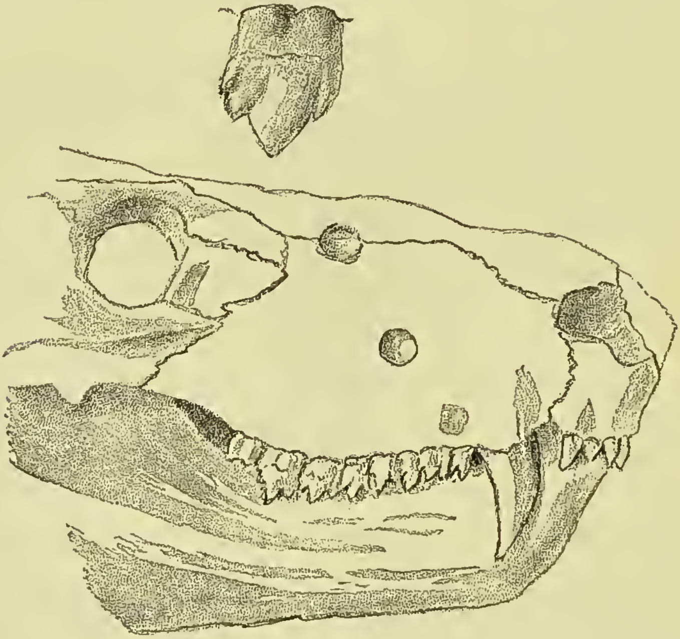
Of the Therochelonia, so styled on account of resemblances in the palate to that of Chelonia, the genus Dicynodon of Owen is best known.

In it the only teeth known are two exceedingly long and strong tusks which project down from the upper jaw in the position where canine teeth usually occur; the margin of the toothless mandible was rather sharp, just as in turtles and tortoises, and was, perhaps, covered with a horny bill, as may also have been the maxilla.

Seeley points out that it is not truly a canine because it is implanted some distance behind the premaxillary suture, but this is not of much importance since, for reasons given at a previous page, the canine can no longer be regarded as a morphological entity, and we may hence apply the term to any caniniform tooth; and, as it is implanted in a socket considerably produced, it may easily have commenced its development close to the suture.

The other group, the Therosuchia, present dentitions very varied in character, some (Procolophon) have conical, cylindrical teeth of sub-equal size, with expanded bases in close union with the jaw, and teeth upon the palate; the teeth of the upper and lower jaws interdigitate, and all the usual characters of a reptilian dentition are present.

Fig. 135 (1).



But the main interest lies in the sub-group, the Theriodontia, where for the first time we meet with teeth which may be divided into incisors, canines, and molars, and in which the general appearance of the dentition is distinctly mammalian. Nevertheless the composite lower jaw remains, in the distinctness of its component bones thoroughly reptilian, and the molars show in different forms many gradations between the simple reptilian cones (Ælurosaurus) and the tuberculated many-cusped teeth (Diademodon).

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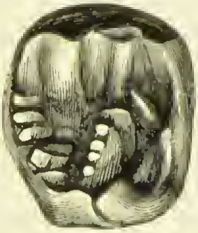
(1) Dentition of Cynognathus (after Seeley), with single upper tooth on large scale; quarter natural size.

A general idea of these dentitions may be gained from the genus Cynognathus here figured. The incisors stand in a rounded curve, and have slightly serrated margins; there are four in each half of the premaxilla, and in the lower jaw there are probably three on each side, the outermost being the largest, as in Carnivora.

There is a diastema in front of the large upper canine, and the lower canine passes up inside it, being received into a deep fossa. Behind the canine follow nine teeth which, on account of the greater simplicity of the first five, may be divided into five premolars and four molars.

Fig. 136 (¹).



The molars have a principal cusp and several subsidiary cusps: the enamel terminates in a distinct margin, and there is a slight hint of a division into two roots; there are, however, no internal cusps, and the upper and lower molars work upon one another with a shearing action.

A point of great interest is that there is an indication of a cingulum, which, in other forms, *e.g.*, Nythosaurus, is well marked. The advocates of the trituberculur theory place the cingulum in a very unimportant position, explaining the genesis of tooth cusps in quite other ways, whereas those who do not accept this theory in its entirety, attribute to the cingulum a much more important *rôle* as the source of additional cusps.

(¹) M_8 of Diademodon × 4. (After Seeley.)

If, then, the theriodonts lie upon, or close to, the direct line of mammalian ancestry, as most zoologists consider that they do, the appearance of the cingulum at so early a period seems significant, for here, according to the one school, are additional cusps *in posse.*

In number the teeth vary considerably; some had as many as six incisors on each side of the upper jaw (Pristerognathus), while others (Deuterosaurus) had the molars reduced to one on each side; two-rooted teeth, not otherwise known amongst Reptilia, appear in Tritylodon. But the molars in some attain to a much higher degree of differentiation, so that Seeley writes of Diademodon that "if its teeth had occurred isolated it would have been legitimate to have referred them to mammals."

These molar teeth are of quadrate form, with two or three cusps on the anterior border, one tubercle on the anterior and several on the posterior border; there is also a tubercle in the middle of the crown. They are usually single-rooted, and often show much attrition. The premolars were small, the canine large and fluted, and the incisors are not known. The premolars were generally small, circular, and tuberculate, but in some allied forms they were laterally compressed.

Some of these reptiles attained to considerable size; thus, Sir Richard Owen ("Quart. Journ. Geolog. Soc.," 1876) described, under the name of Cynodraco, one as large as a lion, which had eight incisors in the lower jaw, of which the first is the smallest, and a canine of moderate size. The upper incisors are not known, but there were a pair of upper canines of such size that they extended down along the outside of a flattened portion of the lower jaw, like the canine teeth of Machairodus and those of Dinoceras. This protection of an especially long upper tooth by a corresponding downgrowth of the lower jaw is by no means an unusual provision of nature. Besides being met with in the instances cited, it is seen in Tinoceras, another of the Dinocerata, and in Chauliodus, a deep-sea fish dredged up by the "Challenger." It is, however, not a universal structure, as it is quite absent in the musk deer. The hinder margins of these canines were trenchant and finely serrated. The molar teeth are not known.

No indication of any succession of teeth has so far been found in any of the Anomodonts.

A genus to which the name Anomodon has been given had nothing but two tusks in the upper jaw, the lower being wholly edentulous, and the Placodontia had incisor-like teeth, in front, with rounded, flattish teeth at the back, the palate being furnished with similar teeth.

It has been mentioned that the lower jaw consists of all the usual components of the reptilian jaw, but the dentary bone forms so large a proportion of the whole, that it is suggested that this is the chief element in the mammalian jaw.

The Pterosauria, or flying reptiles, have, since the discovery of toothed birds, become of special interest to the odontologist. The wings were stretched membranes, like those of a bat, and the measurement across their tips in some of the largest must have been twenty-five feet; but most of those known were much smaller, from ten to fifteen inches in total length of body. In the Pterodactyls the jaws are furnished with long, slender, sharp teeth in their whole length; but in Ramphorhynchus the anterior extremities of the jaws are without teeth, and it has been conjectured that these portions were sheathed in horny beaks.

And Professor Marsh ("American Journal of Science," 1876) has discovered, in the same formation in which he found the toothed birds, several species of Pterodactyls wholly without teeth, for which the generic name Pteranodon is proposed.

The jaws, which are more like those of birds than those of any known reptile, show no traces of teeth, and the premaxillaries seem to have been encased in a horny covering.

THE TEETH OF BIRDS.

Prior to the discovery by Professor Marsh, of Yale College, in 1870, of the remains of birds with teeth in the cretaceous formations of Western Kansas, little was with certainty known about the existence of teeth in any bird, although one or two fossils, leading to the suspicion that birds might have possessed teeth, were known. The state of knowledge up to that time has been clearly summarised by Mr. Woodward ("Popular Science Review," 1875), to this effect: that it had been long supposed that no examples of teeth were to be met with amongst the birds, although some, such as the Merganser, have the margins of the bill serrated, so that the functions of teeth are discharged by this horny armature of the jaws.

The point of the bill is hooked, and for a little way behind the point is smooth, the corresponding part of the lower bill being also smooth. The lower bill is furnished with one row of pointed horny teeth, which fit in between two rows on the upper bill, the latter raking backwards.

They are apparently horny near the apices, there are some fine canals, and each is seated upon a vascular papilla; their bases coalesce, so that there is a continuous horny sheath to the jaw.

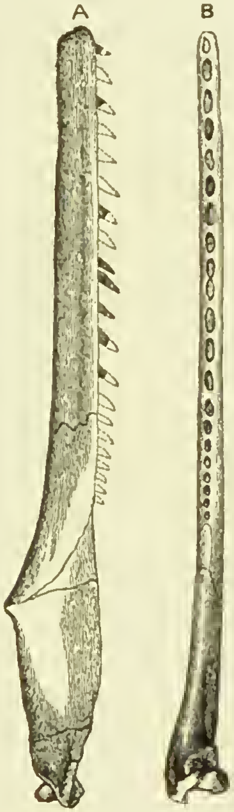
It has been said that bony prominences correspond to these so-called teeth, but in the specimen which I examined I could see no trace of such a thing.

In the fossil bird described by Professor Owen, from the London clay, under the name of Odontopteryx toliapicus, the form of the bill is not known, but the margins of the jaws are furnished with strong bony prominences. And Geoffroy St. Hilaire had described a series of vascular pulps as existing on the margin of the jaw of parroquets just about to be hatched, which, though destined to form a horny bill, and not to be calcified into teeth, yet strikingly recall dental pulps. Then there is also the famous fossil Archæopteryx, an anomalous oolitic bird, with a long and jointed tail, which possessed teeth. In the first specimen described there was a flaw in the evidence, inasmuch as the toothed jaw was not *in situ*, and so possibly might have belonged to another creature, but in the specimen now at Berlin there can be no question as to this.

In successive expeditions, conducted under great difficulties owing to the extremes of heat and cold, and to the hostility of the Indians, the remains of no less than one hundred and fifty different individuals referable to the sub-class ODONTORNITHES have been obtained by Professor Marsh; they are classified under nine genera and twenty species.

FIG. 137 (1)

1½ N.S.



They are referable to two widely different types, one group consisting of comparatively small birds, with great power of flight, and having their teeth implanted in distinct sockets (Odontotornæ, illustrated by the genus Ichthyornis as a type); the other group consisting of very large swimming birds, without wings, and having teeth in grooves (Odontoleæ, type genus Hesperornis).

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(1) Mandible of Ichthyornis. (After Professor Marsh.) A. Side view, showing the teeth *in situ*. B. View of upper surface, showing the sockets in which the teeth were implanted.

In Ichthyornis the teeth were about twenty-one in number in each ramus, all sharp and pointed, and recurved; the crowns were coated with enamel, and the front and back edges sharp but not serrated.

They are implanted in distinct though shallow sockets, and the maxillary teeth are a little larger than those opposing them; the premaxillaries were probably edentulous, and perhaps covered with a horny bill.

In the lower jaw the largest teeth occur about the middle of the ramus, those at its posterior end being materially smaller; and the sockets are deeper and stronger than in the upper jaw. The succession takes place vertically, as in Crocodiles and Dinosaurs.

The genus Hesperornis, probably diving birds, includes species six feet in length: as has already been mentioned, the teeth are not implanted in distinct sockets, but lie in a continuous groove like those of Ichthyosaurus; slight projections from the lateral walls indicate a partitioning off into sockets, but nothing more than this is attained, and after the perishing of the soft parts the teeth were easily displaced, and had often fallen out of the jaws. The premaxillary is edentulous, but the teeth extend quite to the anterior extremity of the lower jaw: in one specimen there are fourteen sockets in the maxillary bone, and thirty-three in the corresponding lower ramus.

The successional tooth germs were formed at the side of the base of the old ones, and causing absorption of the old roots, migrated into the excavations so formed, grew large, and ultimately expelled their predecessors, as is seen in the accompanying figure.

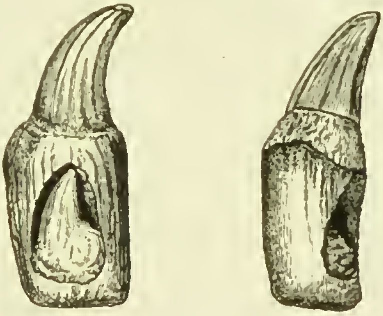
In structure these teeth consist of hard dentine, invested with a rather thin layer of enamel, and having a large axial pulp cavity. The basal portion of the roots consists of osteo-dentine.

The outer side of the crown is nearly flat, the inner strongly convex: the junction of these surfaces is marked by a sharp ridge, not serrated.

In form the teeth of Hesperornis present a close resemblance to those of Mosasaurus, a great extinct lizard.

Indeed, as Professor Marsh observes, "in all their main features the teeth of Hesperornis are essentially reptilian, and no anatomist would hesitate to refer them to that class, had they been found alone. Combined with the other reptilian characters of Hesperornis . . . they clearly indicate a genetic connection with that group."

FIG. 138 (¹).



In the dentine contour lines are abundant; the enamel is so dense as to appear structureless, and there is no coronal cementum.

The foregoing account is condensed from the magnificent volume published by the United States Government Geological Exploration. (Odontornithes, a Monograph, &c., by O. C. Marsh, Professor of Palæontology, Yale College.)

With these notable exceptions, the jaws of all known birds are toothless, the horny cases forming their beaks taking the places and fulfilling the functions of teeth.

(¹) (After Professor Marsh.) A. Hesperornis regalis, with successional tooth in an excavation at its base; enlarged eight diameters. B. Tooth of Mosasaurus princeps, half natural size.

The evidence that true teeth might possibly become replaced by horny teeth, these again coalescing with their neighbours to form a horny casing, has been given at p. 239.

It would therefore seem possible that the ancestral birds all had true teeth, and it is possible that a sufficiently extended search might reveal rudimentary teeth surviving beneath the functional horny bill, or even possibly above it, like those of Ornithorhynchus. Indeed Röse has found that in Sterna the tooth band exists, though no rudiments are to be found of more differentiated tooth germs; though, judging from his figures, some might doubt the propriety of identifying so small an inflection of epithelium as being with any certainty a rudimentary tooth band.

CHAPTER IX.

THE TEETH OF MAMMALIA.

The ancestry of the Mammalia remains still somewhat uncertain, and the Theriodont reptiles are probably not in the direct line of descent, though they present certain resemblances to mammals, and are perhaps not far from the stem.

The mammalia are usually now divided into three groups —**Prototheria, Metatheria,** and **Eutheria.**

The Prototheria comprise but few animals numerically, as no extinct forms are known, and of living animals only two families exist, namely, the Ornithorhyncidæ and the Echidnidæ.

They stand at the bottom of the mammalian class, and present many points of affinity with lower vertebrates, particularly with Sauropsida and Batrachia.

Recent discoveries have added fresh interest to, at all events the Ornithorhyncus, which has been found to lay eggs, and to be possessed of a unique arrangement of teeth.

Metatheria, like the preceding group, have characters which place them low in the mammalian scale, but they are numerously represented at the present day, comprising the animals known as Marsupials, which practically monopolise the Australian region, and exist also in the American continent. In former times they existed over other portions of the globe, and some of the earliest mammalian fossils are perhaps referable to the group.

Eutheria comprise all the mammals in whom the young are nourished by means of a placenta.

It must not be supposed by the student that the *Metatheria* of the present day are descended directly from the

Prototheria, or that the *Eutheria* are direct descendants of the marsupials; it is more probable that exceedingly early and quite unknown mammalian forms have given rise to each of these stems, and that the *Prototheria* have advanced but little, the marsupials a good deal, giving rise to a large number of forms, while the *Eutheria* have far outstripped the others, and have been and are supplanting them in all directions.

PROTOTHERIA.

The Echidna is, so far as is known, entirely edentulous.

The Ornithorhyncus, which in its soft parts and skeleton alike differs from higher mammals in points which approach the characters of Sauropsida, is furnished with wide flattened jaws, in which horny plates fulfil the function of true teeth; from this peculiarity comes its name of duck-billed Platypus.

Recently Mr. Caldwell discovered that it, though possessed of functional mammary glands, lays eggs, and more recently still Mr. Poulton found that at an early stage tooth germs were present, as he supposed, underneath the horny plates. Following upon this Mr. Oldfield Thomas found that its true teeth came into actual use, and that they were not beneath but above the horny plates.

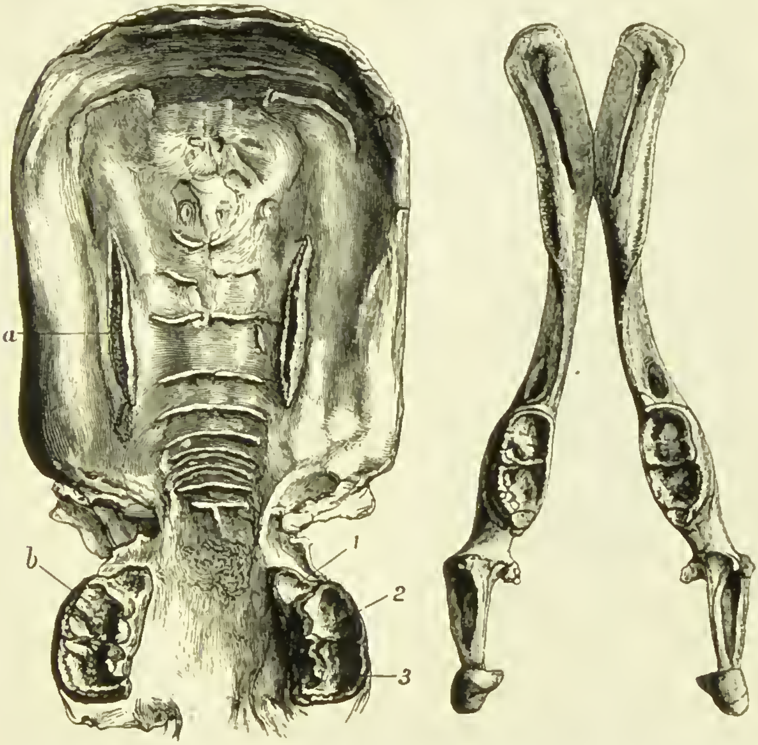
To take first the dentition, if such it can be called, of the adult animals; the horny plates with which the jaws are ultimately furnished are four in number in each jaw, the anterior plate being a thin long band with a longitudinal ridge and a furrow in its inner side, and the posterior plate a flat broad-topped mass, the surface of which is roughened by a series of ridges separated from one another by concavities, the ridges of the opposing plates interdigitating with one another.

These plates are simply pronounced thickenings and hardenings of the oral epithelium, and their under-surfaces are penetrated by long papillæ, each of which sends up a prolongation of soft, deeply-staining cells from its apex.

The plates are at their sides quite continuous with the stratum corneum of the epithelium, of which their harder portions are composed; there is no calcification, and no bony structure in them. Somewhat similar horny structures occur upon the tongues.

A full account of the structure and form of these plates will be found in a paper by Mr Poulton ("Quart. Journ. Microscop. Science," Vol. XXIX., N.S.), which is devoted to a full description of his most interesting and significant discovery of the existence of the true tooth germs which he believed to underlie the forming horny plates.

Fig. 139 (¹).



(¹) Upper and lower jaws of Ornithorhyncus. From the lower jaw the skin, &c., has been removed, but it remains upon the upper. *a*. Anterior horny plate. *b*. Posterior horny plate, with remains of tooth sockets, 1, 2, 3.

From the want of material he was somewhat uncertain as to the extent to which the calcification of these teeth goes, and what afterwards becomes of them, but he saw that there were the germs of four teeth in the upper, on each side, and probably the same number in the lower jaw; and they occupy a widely open furrow, which he thought was subsequently occupied by the horny plate.

Fig. 140 (1).

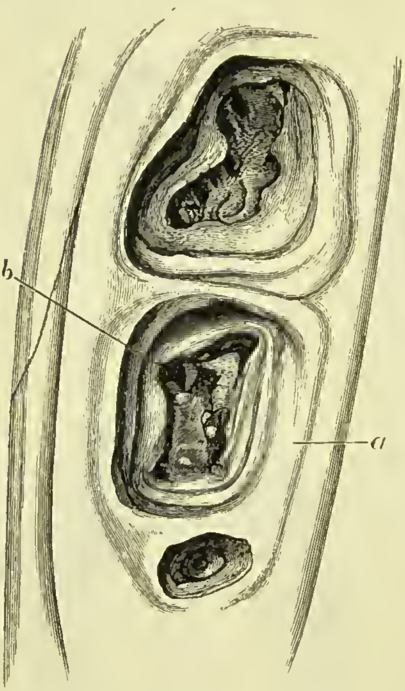
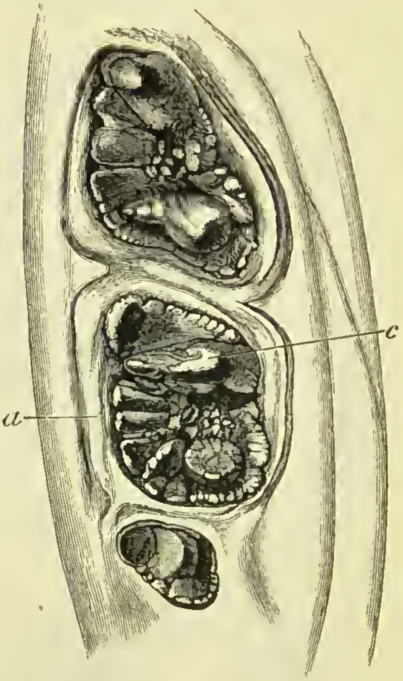


Fig. 141 (2).



In this connection it is interesting to note that Professor Huxley, in writing of the Monotremes, had years ago expressed the conviction that there is good reason to suppose that edentulous forms are modified descendants of toothed forms.

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(1) Horny plate, *a*, of a half-grown Ornithorhyncus, with empty pits; *b*, for the reception of the teeth.

(2) Horny plate with teeth *in situ*. *c*. Long cusp of tooth, after Professor Stewart, from a specimen in the Royal College of Surgeons' Museum.

Mr. Oldfield Thomas and Professor Stewart subsequently found that the true teeth of Ornithorhyncus are cut, and for a time are in actual use; they are twelve in number, two on each side being of some size, and the third very small. The upper teeth have broad-topped crowns, with two long cusps on the inner edge, and a crenated border along the outer edge with many small cusps; in the lower this is reversed. They have low broad crowns with short stunted roots, by which, however, they are for a time pretty firmly held. Instead of being beneath the horny plates they are on the top of them, and their implantation is peculiar; the expanded crowns narrow rapidly at the neck, and they are surrounded by a very dense and thick epithelium, almost horny, which rises into a ring round them and dips underneath the expanded portion, so that the tooth lies in a sort of cup of horny consistency.

This cup is not complete at the bottom, but the roots pass through it and fit depressions in the bone, which is perforated by foramina for their vessels and nerves. When the creature is about twelve inches long the teeth are shed, and then the horny cups grow in underneath and become complete; thus the curiously cupped and sculptured surface of the horny plates which have been so long familiar has its form determined by once having formed the bed for a tooth with several roots, and although the horn grows underneath and fills up the holes for the roots to go through, yet the old general form is more or less maintained by the horny plate which serves as the organ of mastication throughout the rest of life of the animal.

So far as is known, this is an arrangement quite unique amongst mammals, or indeed any other tooth-bearing creatures.

The horny plates are therefore not at all to be regarded as horny teeth, but they are epithelial structures which take the place of the teeth after these are shed, and therefore they are not closely homologous with the horny teeth of lampreys and myxinoids.

The true teeth consist of a body of dentine, with a central pulp cavity, capped with thin but hard enamel, and implanted by short roots; the breadth of crown greatly exceeding its vertical dimension.

The enamel is apparently of simple structure, and the dentine is permeated by fine dentinal tubes and beset with a wonderful number of interglobular spaces, which in parts of the crown mask its tubular structure. In the principal cusp larger, apparently vascular, canals exist, and as one approaches the stunted roots, a somewhat abrupt transition in structure takes place, all dentinal tubes disappearing and large lacunæ appearing.

The roots are hence of softer, coarser material than the crown, which itself is not of a high type of dentine structure.

Thus the dentine structure of the tooth is somewhat that which we are accustomed to see as a result of pathological processes, and would suggest, so far as it goes, that the Ornithorhyncus tooth has degenerated from some earlier and more complete tooth-form in which the roots consisted of properly developed dentine.

I am not acquainted with any example of this degeneration in the type of dentine formation as the root portion of the tooth is approached in any other mammalian tooth: in those teeth which have no roots, if such an expression may be allowed, but which are about to become anchylosed to the bone, something of the kind may be seen. (Cf. also the tooth of Hesperornis, p. 296.)

The British Museum specimen described by Mr. Oldfield Thomas ("Proc. Roy. Soc.," May, 1889) (1), shows that the teeth were subjected to severe attrition, as one which was about to be shed was worn as thin as paper. No tooth, fossil or recent, corresponds in naked-eye characters with that of Ornithorhynchus, though that of the mesozoic Microlestes does so in some degree, so that Mr. Oldfield Thomas gives a figure of it for comparison.

Microlestes has generally been looked upon as a marsupial, allied to Plagiaulax, though Professor Cope has suggested that all the group of multituberculate toothed Mesozoic mammals may have been monotremes.

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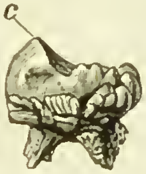
(1) An interesting discussion on the significance of the teeth of Ornithorhynchus, by Professor St. George Mivart, will be found in the "Proc. Roy. Soc.," 1888.

But a microscopic examination of a tooth of Microlestes, which Mr. Poulton kindly allowed me to make, shows no close resemblance to the recent marsupials, for the enamel is not clearly penetrated by dentinal tubes, nor does it present the peculiarities of structure found in Ornithorhynchus. Thus its structure gives no help, but rather goes to render still more indefinite its probable zoological position.

Though there is no doubt that the Ornithorhynchus tooth reveals to us a tooth of a period very remote in point of time, it has yet by no means a simple crown, and it does not help us in knowing anything which can be regarded as a primitive parent form whence all mammalian teeth may have been derived.

FIG. 142 (¹).



Still the discovery is of incalculable value, inasmuch as many of the early mammalia are known to us only by teeth, and the form and structure of a monotrematous tooth gives us something far lower in the evolutionary scale than had hitherto been known.

The Echidna, or scaly Ant-Eater, also an Australian mammal, has no teeth whatever, so far as is at present known.

EUTHERIA.

There is great difficulty in arranging Placental Mammals in any order of sequence, inasmuch as those now existing,

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(¹) Molar tooth of Ornithorhynchus. *c*. Long cusp.

and those fossil forms known to us form but a small fraction of all which have once existed. And although no modern naturalist can well doubt that all existing mammals are lineal descendants of a smaller number of forms previously existing, yet they do not admit of being arranged on any one stem, and are not at all lineal descendants of one another.

In "Mammals Living and Extinct," by Flower and Lydekker, they are grouped provisionally, and for want of a better arrangement, thus :—

Edentata—Sloths, Ant-Eaters, Armadillos, &c.
Sirenia—Sperm Whales, Porpoises, Whalebone Whales, &c.
Cetacea—So-called Herbivorous Cetacea, Manatee, Dugong, &c.
Ungulata (Hoofed Mammals)—
  Artiodactyla—Pigs, Hippopotamus, Camels, Ruminants, &c.
  Perissodactyla—Tapirs, Horses, Rhinoceros, &c.
  Toxodontia, *Amblypoda*—Extinct animals from American Eocene formations.
  Hyracoidea—Hyrax.
  Proboscidea—Elephants, Dinotheriums, &c.
  Tillodontia—An Eocene group with affinities to several other groups, *i.e.*, to Rodents and Carnivora, as well as to Ungulates.
Rodentia—Hares, Rabbits, Rats, &c.
Carnivora vera—Cats, Dogs, Bears, &c.
Carnivora pinnipedia—Seals, Walrus, &c.
Chiroptera—Bats.
Insectivora—Hedgehogs, Moles, &c., &c.
Primates—Man, Monkeys, and Lemurs.

The mixed and uncertain affinities of some groups render any simple linear classification unsatisfactory, but two other methods may be attempted : the "circular," in which animals are grouped round generalised types, and what may be termed the phylogenetic, in which animals are arranged according to their descent, in which case we should have a parent stem branching, and the branches subdividing again and again.

If we really knew the lines of descent of Mammalia, the latter is, of course, the more logical, but as no two authorities quite agree, it is for the present only partially practicable.

Dr. Wortman writes : "We know, for example, that the Primates could not be the ancestral group, for the obvious reason that they do not extend beyond Miocene time ; nor the Carnivora, which appeared about the same time ; nor the Rodentia, which date from the Middle Eocene ; nor the Chiroptera, which can be traced back no further than the Upper Eocene. We are, therefore, restricted in our choice to the Insectivores, Lemuroids, Creodonts, or Tillodonts, which alone of the entire series continue backwards to the base of the Eocene period. With reference to the Creodonts, I do not believe that any important distinctions exist between them and the Insectivores, while the line between this latter group and the Lemuroids and Tillodonts becomes exceedingly shadowy at this point."

That the Insectivora are a very ancient and generalised group all naturalists agree, and the Lemuroids also go very far back.

And though questions of classification are foreign to the subject of this work, yet, inasmuch as the teeth are a very important criterion of affinity, it is desirable, but exceedingly difficult, to arrange an account of the dentitions in anything approaching to a logical sequence.

CHAPTER X.

INTRODUCTORY REMARKS.

Before proceeding to the description of the teeth of Mammals, of which it is only possible to give the barest outline, it seems desirable to devote a few pages to those general principles which underlie, and render interesting and intelligible, the details with which we shall be concerned.

Before the day of Darwin it was customary to explain those resemblances and points of identity which the study of comparative anatomy revealed, upon the supposition that there was some sort of type or standard organisation, and that all others were arrived at by modifications and departures from this type, these modifications being introduced with a direct purpose in view, in order to fit the creature to a special habit of life.

Among the matters which this "type" theory sought to account for was this: when an animal possesses some peculiar organ, it is found on close examination that it, however specialised, is after all only something which allied animals also possess, only it has been exaggerated or developed in an unusual manner and degree; or, on the other hand, that when an organ is wanting, the suppressed organ is not absolutely abolished, but is usually to be found stunted and in a rudimentary condition, instead of in its ordinary size and functional activity.

This is as true of teeth as of any other organs; indeed they afford many admirable examples of the law.

Thus the tusks of the boar or of the Sus babirussa, large and peculiar though they be, are not new developments, but are merely the canine teeth which all pigs possess, but which in this species attain to unusual dimensions. In the same way the enormous straight tusk of the male Narwal is nothing more than an incisor tooth of one side, the fellow to which has been checked in its development; but this is not missing, for it remains throughout the life of the animal buried within its socket. In the female Narwal both of the teeth being rudimentary, are permanently enclosed within the sockets, and are, of course, not of the smallest service to the animal, directly or indirectly; furthermore, as has been shown by Professor Sir W. Turner, in young specimens, a second pair of rudimentary aborted incisors are to be found, which in the adults have disappeared.

The modern school of biologists, rejecting the "archetype" theory, refer these correspondences detected between dentitions upon the whole dissimilar to one another to a more intelligible cause, namely, inheritance. Assuming, as every evidence compels us to assume, that the many divergent forms which we observe have been derived by progressive modifications and differentiations from fewer and simpler ancestral forms, we shall have no difficulty in seeing how, by such processes as we full well know to occur, namely, the dwindling of disused organs and the exaggerated development of those very useful, great differences may ultimately result.

To illustrate what is meant by this so-called "adaptive modification," this suppression of things that are not needed, and increased development of those most used, we may recur to the dentitions of non-venomous and venomous snakes.

In them we saw that the typical dentition in the snake, as exemplified by the Pythons, consisted of two complete rows of teeth in the upper jaw, one of which occupied the maxilla, and one row in the lower. Then in the Colubrine Opisthoglypha some of the maxillary teeth become enlarged and grooved, while the snakes are only doubtfully poisonous; then, further, in the Proteroglypha the front teeth of the maxilla become grooved and enlarged, the complete row of maxillary teeth gets reduced to a few small teeth behind the poison fang, and the maxilla gets reduced in antero-posterior extent, while the snakes are all venomous.

Finally, in the Vipers the poison fang is enormously developed, the rest of the maxillary teeth are lost, and the maxilla so shortened down as to be about square, while coincidently it acquires a movement of rotation through a large angle, so as to lay the poison fang down flat, when not in use. This mobility of the maxilla was foreshadowed in the Cobra, in which the bone was slightly movable. And the same serial modification is to be observed in the poison fangs (p. 282) which range from the very complete canal of the Vipers, through the closed groove of the Cobra, to the open grooves of some of the other Proteroglypha.

Thus there can be found amongst living snakes a most complete chain of transitional forms of poison apparatus.

But in many poisonous colubrine snakes the three or four small and useless teeth lingering upon the maxillary bone long after their function was gone, served to indicate to us in some measure the gradual process by which that singularly perfect adaptation of means to an end, the poison apparatus of the viper, was arrived at.

Good examples of rudimentary teeth are to be found in the larval teeth of the edentulous sturgeon, or of the whalebone whales, or in the teeth buried beneath the horny plates of the deflected portion of the Dugong's jaw, all of these being of absolutely no service to their possessors. Some teeth have disappeared utterly; thus the upper incisors of Ruminants are gone, and no rudiments exist at any stage; others still remain in a stunted and dwindled form, and do not persist throughout the lifetime of the animal, as for instance the first premolars of a horse, or two out of the four premolars of most bears.

The teeth of Ornithorhynchus do work for their possessor till it approaches its adult size: then they are curiously supplanted by a horny development of the gums.

Mr. Darwin has proved that any modification in the structure of a plant or an animal, which is of benefit to its possessor, is capable, nay, is sure, of being transmitted and intensified in successive generations, until great and material differences have more or less masked the resemblance to the present form.

Just as man, by picking out and breeding from those modifications of form, &c., that please him best, has been able, in the course of a few years—in a length of time altogether infinitesimal, as compared with the time during which the surface of land and sea has been of pretty nearly its present form, to say nothing of the enormously longer earlier geological epochs—to profoundly modify the breeds of dogs, of horses, and of numbers of plants, all of which are absolutely known to have had a common origin, so in nature forces are and ever have been in perpetual operation, which effect the same thing.

A pigeon-fancier wants a pigeon of particular plumage, with a few feathers a little different from any pigeon he has ever seen or heard of (1) ; he knows by experience that little variations are for ever arising, and that by watching a sufficient number of young ones, and rigorously picking out those which at all tend in the direction of what he wants, he will get what he wants, and will even tell you with confidence that in so many years he will make a breed with the peculiarity desired. And exactly as the plumage that was wanted is got, so in nature the tooth that is "wanted," *i.e.*, the dentition that is excellently well adapted to do its work, by the operation of that law known as "survival of the fittest" may have been elaborated.

For the number of animals born, or of seeds germinating, is vastly in excess of the capabilities of the area in which they live to support, so that a weeding-out process, the death of a large number, is a necessity. And those are the most likely to die or to fail to breed, which are in any way placed at a disadvantage.

It is, therefore, quite enough that one of the small variations for ever arising in animals shall be of advantage to it, for us to see how the peculiarity is likely to be transmitted and intensified in successive generations without the intervention of man.

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(1) An eminent pigeon-fancier, Sir J. Sebright, told Mr. Darwin that he could produce any given feather in three years.

The question has been well presented by Mr. Wallace, who points out that we must not think so much of variations in individuals as in groups of individuals: for instance, it is a familiar fact that people vary in height, so that any hundred persons may be divided into fifty taller and fifty shorter persons. Now if a little extra height were of advantage, many or most of the fifty would experience it, though some might not. In the same way, if we grouped one hundred animals whose teeth varied a little in respect of strength into the fifty weaker and the fifty stronger, it is easy to see that the stronger fifty would get the better of the others in the struggle for existence on the whole, would be more certain to propagate their kind, and would repeat in a majority of their progeny those peculiarities which had helped themselves to live.

Thus the doctrine of natural selection or survival of the fittest is as fully applicable to the teeth of an animal as to any part of its organisation, and the operation of this natural law will be constantly tending to produce advantageous or "adaptive" differences. On the other hand, the strong power of inheritance is tending to preserve even that which, in the altering conditions of life, has become of very little use, and thus rudimentary teeth we may understand to be teeth which are in process of disappearance, having ceased to be useful to their possessors, but which have still for a long time lingered upon the scene. And it must be remembered that, just as natural selection brings an organ up to its fullest standard of efficiency, so the cessation of selection will tend to allow its variations in a downward direction to establish themselves. In other words, the continuance of that selection which elaborated an organ is required to maintain it at that standard.

For the efficient action of natural selection, it will be seen that two conditions are essential: the one a competition amongst the organisms concerned, and the other a tendency to vary, the variations being capable of its being inherited.

Now, however produced, it is a familiar fact that variations occur, and that they are capable of perpetuation, as every florist or breeder of animals knows.

It was formerly supposed that the variations seized upon by natural selection and intensified in successive generations were of necessity small, so small that it was difficult to see how their advantage would really be felt.

But since attention has been drawn to this subject, and careful measurements and weighings have been taken of large numbers of wild specimens of the same species, it has been found that the variations are often far from being insignificant in extent.

Then Mr. Wallace ("Darwinism," 1889) points out that the variation in common species reaches often 20 per cent. of the size of the part implicated, and this without reference to the general size of the animal. As an example may be taken the jaws of the wolf, which in ten specimens varied to the extent of an inch and a half in length. If there be an advantage in it, it is easy to see how in a few generations a very distinct advance in the direction of length or shortness of jaw might be established.

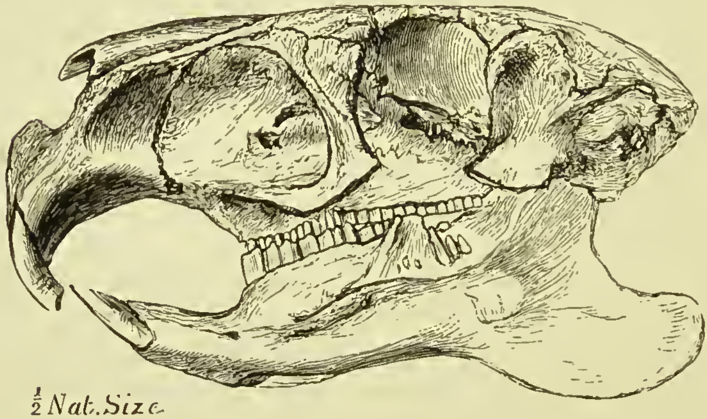
The same species will be found to vary in size according to the locality whence it has come: thus species having a large range in latitude, will generally be found larger in its northern than its southern areas.

Variability in the number of teeth is much more common than has generally been supposed: thus Bateson ("Proc. Zool. Soc.," 1892) found supernumerary teeth in 8 per cent. of the jaws of Gorilla, Orang, and Chimpanzee which he examined. In Phocidæ supernumerary teeth were present in 7 per cent. of the specimens examined, in 4 per cent. of Otariidæ, in 3 per cent. of wild Canidæ, in 8 per cent. of domestic Canidæ, in less than 2 per cent. of wild Felidæ, but in 9 per cent. of domestic Felidæ.

Before leaving this section of our subject, an instructive illustration of the operation of these agencies may be given.

It is very easy for us to see how a "rodent" type of dentition is beneficial to its possessor by rendering accessible articles of food wholly unavailable for creatures which have no means of gnawing through a shell or other hard body. Now it happens that in three regions of the world, pretty completely cut off from one another, three animals, in parentage widely dissimilar, have arrived at dentitions of "functionally rodent" type.

Fig. 143 (¹).



Thus in Australia, a region practically wholly monopolised by Marsupials, a marsupial, the Wombat, has a dentition very much like an ordinary placental Rodent. In the island of Madagascar, one of the very few parts of the globe without indigenous rodents (except a few Muridæ), a Lemurine animal, the Cheiromys, has a dentition modified in a similar direction (though it is probably employed to get at a different sort of food); and elsewhere, scattered all over the world, we have the ordinary Rodents.

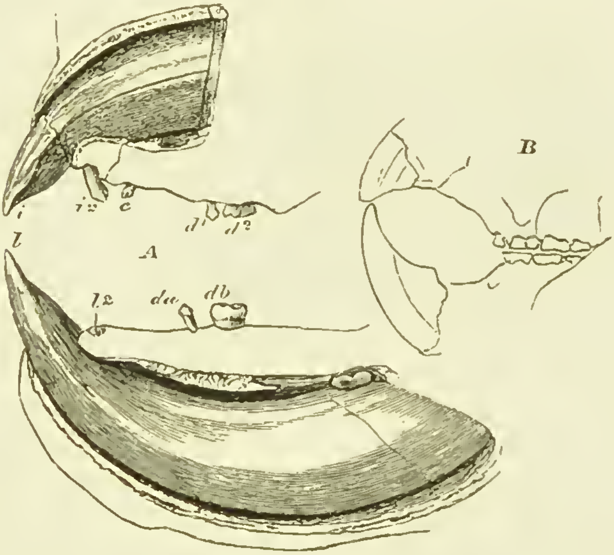
In fact, three sets of creatures, as widely different from each other in parentage as they well could be, have been modified by natural selection until they have dentitions, by no means identical, but for practical purposes not unlike.

It is impossible to conceive that these three creatures

(¹) Skull of a placental rodent (Capybara), showing general character of a rodent's dentition.

have had any recent community of origin: their ancestry must have been widely different, the regions in which they live have been isolated from one another for countless years, and yet they have each got to a "practically rodent" type of dentition. Of extinct Lemurs little is known, and of the ancestry of Cheiromys nothing; but in the compact group of Marsupials, still living in Australia, we are able to dimly see some of the progressive steps which seem to tend toward this rodent form of dentition. In Australia, roughly speaking, there are nothing but Marsupials; in Madagascar more Lemurs than anything else; and in each case, out of the material at hand, natural selection has manufactured a "rodent" dentition.

Fig. 144 (1).



At the same time the force of inheritance is seen in each of them retaining characteristics of the groups whence they have been derived, so that underlying the *primâ facie* resemblance in the teeth, there are points in their several dentitions whereby the wombat shows its marsupial affinities, and the Aye-aye its quadrumanous affinities.

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(1) A. Milk teeth of the Lemurine Cheiromys, with the permanent incisors just coming into place. It differs from any rodent by having many milk teeth. *i.* Permanent incisor. *i* 2. Permanent deciduous incisor. *c.* Deciduous canine. *d*, *d* 2. Deciduous molars. *l.* Lower permanent incisor. *l* 2. Lower deciduous canine. *d a*, *d b*. Lower deciduous molar. B. Reduced outline figure of its permanent dentition, in which it closely mimics the true rodents.

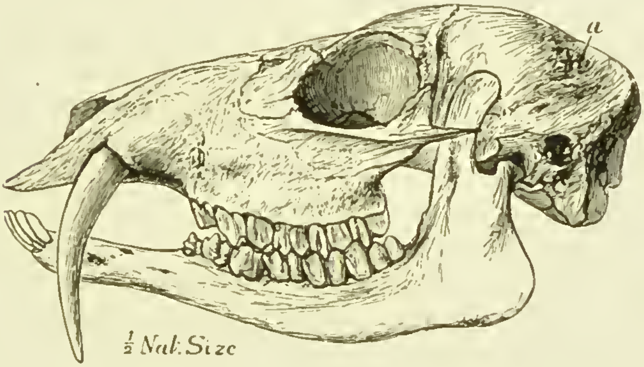
An example of the same sort of thing is seen in the occurrence of hinged teeth in various families of fish (see p. 224), in which the requirements of a hinge and of a means for restoring the bent-down tooth to the upright position are attained by different mechanism according to the difference in the raw material, if such an expression may be allowed.

The approximation to a rodent type of dentition by a number of widely different animals has led to the suggestion being made, that it does not follow that all existing Rodents have had a common origin. Thus Oscar Schmidt ("Mammalia," Internat. Scientif. series, p. 291) writes:—"A comparison of the very different shapes of the molars in the Rodents among one another, and the approximation of many genera—not as yet decided Rodents—to the Rodent type (for instance the Wombat, the fingered animal—Aye-aye—, and the rock coney) render it extremely probable that even our present Rodents are not of one and the same origin. The fact remains, animals of different derivation having attained a similar exterior, succeed extremely well in the struggle for existence, or even better, in their endeavour to obtain food. Unlike as they may be, in one point they are incontestably alike, *i.e.*, in the development of continuously growing incisors."

In addition to these modifications which are of direct use to the individual in the way of assisting in the procuring of food, &c., any character which would enable one male to get an advantage over other males, and so render him more certain to propagate his kind, will be sure to be transmitted and intensified.

Thus we can understand how the males of some species have become ornamented; how the males of many birds have come to sing; and what is of more immediate concern to us, how the males of some animals have become possessed of weapons which the females have not. The possession of weapons by the male is strikingly exemplified in the teeth of animals. The males of many frugivorous monkeys have canine teeth much larger than those of the females; they are cut late, coincidently with the attainment of sexual maturity, and are useful to their possessors as weapons in their combats with other males. The male narwal has its single elongated tusk; the male dugong has tusk-like incisors; in the respective females these same teeth are insignificant.

FIG. 145 (1).



But the most striking instance of the teeth being modified, so as to serve as weapons for sexual combat, is afforded by some members of the group of ruminants, amongst whom, as Cuvier long ago pointed out, those which are armed with horns have no canine teeth, and *vice versâ*—a generalisation which, although subject to slight exceptions, remains upon the whole true.

The male musk-deer (Moschus moschiferus) has canine teeth of enormous length, while it is quite without horns; the female has canine teeth so reduced as to be functionless. The male muntjak, which has very short horns, has canine teeth, but of much smaller size than those of the musk-deer. Other examples of hornless deer furnished with canine teeth are to be found in Swinhoe's water-deer (Hydropotes inermis) and in the Elaphodus cephalophus (which has very small antlers), a Chinese deer more recently discovered, and in the Tragulidæ. It is obvious that males furnished with weapons more powerful than their fellows will be more likely to prove victorious in their battles, to drive away the other males, to monopolise the herd of females, and so to transmit their own peculiarities to offspring, which will again be favoured in the same way. Thus it is very easy to see how, amongst gregarious animals, the development of teeth serving as sexual weapons is likely to be favoured, generation after generation, until canines as highly specialised as those of the musk-deer, or the wild-boar, are attained to.

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(1) Cranium of Moschus, showing the long canine tooth.

It will suffice to indicate to the reader that he must be prepared to find that the teeth are profoundly susceptible of modification, but that, amid all their varied forms, the evidences of descent from ancestors whose teeth departed less from the typical mammalian dentition are clearly traceable in the existence of rudimentary teeth and other such characters. And, although it is by no means probable that we have recognised more than a part of the agencies which are at work, natural selection and sexual selection appear to be competent to produce most of the phenomena of modification observed. There remains one other influence, much more obscure in its nature, to be touched upon, namely, "correlation of growth" or "concomitant variation." When we find that when horns are developed canine teeth are absent; or that, after a boar has been castrated, his tusks cease to grow, although we may be quite unable to conceive the precise manner in which the one thing influences the other, we can see that there is a consistency in the development of the sexual weapon ceasing coincidently with the destruction of the sexual apparatus, or in the fact that two kinds of weapon are not developed in the same animal.

But there are some correlations of growth of a still more recondite nature, in which the connection is less obvious. Of this nature is the relation which exists between peculiarities of the skin and of the teeth: the Edentata, abnormal in their skins, are different from most other Mammalia in their teeth; whales, yet more aberrant in the nature of their skins, have only rudimentary teeth, in the place of which, after birth, plates of whalebone are found.

Mr. Darwin ("Animals and Plants under Domestication,") has collected a number of curious instances of relations existing between hair and teeth. In general terms it may be said that any great abnormality in the hair goes hand in hand with an abnormality of the teeth. Thus, there is a breed of dogs found in Turkey which is almost hairless, and which has very few teeth, the dentition being reduced to a single molar on each side, together with a few imperfect incisors; (1) and in the human subject inherited baldness has been often found to be associated with inherited deficiency of the teeth.

But we must not go further than to say that great abnormality of hair goes hand in hand with abnormality of teeth, for examples have just been given of absence of hair and absence of teeth; and, on the other hand, redundance of hair has in several cases been accompanied by absence of teeth.

Thus, in the case of the now famous hairy family of Burmah, the peculiarity of silky hair being developed over the face was transmitted to a third generation, and in each case the teeth were very deficient in number. A year or two ago a hairy man and his son, said to have come from the interior of Russia, were exhibited in London, and they were almost toothless. (2)

A good many years ago a hairy woman (Julia Pastrana) was exhibited in London, of whom it has commonly been reported that she had an excessive number of teeth. Certain it is that her mouth was very prominent, and that she was described as "dog-faced" and "pig-faced," but models have been presented to the Odontological Society by Mr. Hepburn, which are indisputably known to be models of her mouth, and these do not show any excessive number of teeth. The teeth, at least such of them as can be seen, are enormously large, but the mouth is affected with general hypertrophy of the gums and alveolar processes to such a degree that only a few of the teeth can be made out.

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(1) I have lately described an example of great reduction of the teeth in an individual specimen of the very hairy monkey Colobus caudatus. ("Trans. Odont. Soc.," 1897.)

(2) The man's mouth exemplified the dependence of the growth of the jaw upon the presence of teeth. Ordinarily the increase in size between childhood and adult age takes place by a backward elongation, which allows for the successive development and eruption of the molars behind the spaces occupied by the temporary teeth. But this man never had any true molars, and no such backward elongation of the jaw had ever taken place, so that, though he was a full-sized man, his jaw was no larger than a child's.

But this does not make her case the less interesting to the odontologist, for in the huge teeth, the enormous papillæ of the gum, and the redundant hairs on the face, we have evidence of a disposition to hypertrophies of the integument affecting in different places the different tegumentary appendages which happen to be there. And that the teeth are dermal appendages has been shown at a previous page. (See p. 2.)

He would indeed be a rash man who ventured to assert that he had recognised all the agencies which are at work in the modelling of animal and vegetable forms; but it is safe to say that, at the present time, we are acquainted with "natural selection," or "survival of the fittest," an agency by which variations beneficial to their possessors will be preserved and intensified in successive generations; of "sexual selection," which operates principally by enabling those possessed of certain characters to propagate their race, while others less favoured do not get the opportunity of so doing; and of "concomitant variation" between different parts of the body, an agency much more recondite in its operations, but by which agencies affecting one part may secondarily bring about alterations in some other part.

And operating in the contrary direction, we have a certain fixity of organisation, so that the power of inheritance is constantly asserting itself by the retention of parts which have become useless, for a time at all events, and by the occasional reappearance of characters which have been lost.

Some rather contradictory statements have been made as to the direct effect of high feeding, improvement of breed, &c., upon the cutting of the teeth, early maturity being of course one of the aims of the improvers of farm stock.

With regard to horses, neither high feeding nor improved breed seems to have made any difference, *e.g.*, a Highland pony at five years has as full a mouth as the most pampered horse. But in cows it seems to be different—thus Highland cattle have all the permanent teeth at four-and-a-half or five years of age, whereas some improved breeds have a full mouth at three years. (Williams, "British Dental Association Journal," April, 1882.)

Professor Brown ("Journ. Roy. Agricult. Soc.," 1881, where may be found much valuable information on this subject,) has been unable to trace any change in thirty years, though, if the older writers were accurate, a real acceleration has taken place over much longer periods.

He, however, quite denies that high feeding, of a litter of pigs, for example, will produce any immediate effect, and strongly lays down that their dentition is a reliable test of age.

From what has been said, the reader will have gathered that in order that evolution may go on, it is necessary first that animals shall vary, and second, that these variations shall be inherited; granted these two propositions, the process is intelligible.

That animals do vary we have already seen, but there are various views current as to the causes of that variation.

One school, which is supported by the very numerous measurements taken of prawns by Professor Weldon (prawns were selected as being creatures of which it was easy to procure large numbers), hold that the variations are, so to speak, fortuitous; that is to say, that they take place round a mean in the same proportions as would result were they determined by the tossing up of a coin, those which are advantageous getting preserved by selection, while those which are not die out.

The other school hold that they are by no means fortuitous, but that they take place along certain defined lines towards which there is an ever acting tendency, and that the force in operation is that of the environment and habits of the animal.

This involves another consideration, namely, whether characters acquired by an animal in its lifetime can be and are transmitted to its progeny. And on this point also naturalists are divided into two camps: those who hold that the agencies enumerated are all-sufficient, and, with Professor Weissmann, hold that qualities acquired during its life by the individual under the influence of outside conditions can never be transmitted; and those, the so-called Neo-Lamarckians, who believe that they can.

Amongst the strongest advocates of this latter view are several of the American naturalists who have given much attention to teeth, and base their arguments largely upon them, especially Professors Cope, Ryder, and Osborn, to whose views I shall have from time to time to recur.

Thus it has been suggested (J. A. Ryder, "Proc. Acad. Nat. Sciences, Philadelphia," 1878), that the pattern of the molar teeth of herbivora is the result of the extent and direction of the excursions of the mandible when it is in use, and so depends upon the form of the glenoid cavity and of the condyle; that hence the greatest modification is to be found nearest to the articulation, where the greatest force is exerted.

Thus "bunodont" animals, *i.e.*, those that have rounded conical cusps upon their short-rooted teeth, have a cylindrical condyle; selenodonts, or those with crescentic ridges on the molars, have a condyle which is expanded and plane, while lophodonts, or those with transversely ridged teeth, have a globular condyle.

And it has been pointed out by Cope that in many instances the articular surfaces of bones assume forms very similar to those which would be modelled by two somewhat plastic masses working upon one another.

But even if we grant the one much disputed point, namely, that characters acquired by the individual in its own lifetime can be transmitted to its offspring, there is a special difficulty remaining in the case of teeth in adopting the simple mechanical explanation that the teeth are so to speak drawn out into their forms, whether in one or in ten thousand generations. For, unlike a bone, which is constantly growing and being renewed after it has come into use, that portion of the tooth which is subject to these direct influences is hard and rigid, and its form, whatever it be, in that individual is unalterable: in order to alter the form of a masticating surface by direct mechanical means, the influence would seem to have to be brought to bear upon the teeth while they are yet soft, when they are still buried within the jaw in their bony crypts. And we cannot safely assume that structures like enamel covered dentine can be altered by pressure, the essential character of dentine being its elasticity, and that of enamel its rigidity.

It therefore follows that the tooth is of a nature very little likely either to be deformed, or being deformed, to retain the deformity.

Cope, quoting my objection, states that Kölliker and others have established the existence of osteoclasts on dentine as well as upon bone, but this in no way appears to me to meet the objection, as the only place where osteoclasts can occur is on the inside of the dentine, *i.e.*, on the walls of the pulp cavity, and I do not see how this can help the matter short of removing the whole thickness of the dentine. Moreover, it appears to me that we have no right to assume that the lateral excursions of the jaw and the form of the condyle antedated the special form of the teeth.

Thus, however tempting the doctrine of Cope's kinetogenesis, by which the very accurate articulation of the cusps of the teeth with one another, as well as their manifold forms is sought to be accounted for, it hardly commends itself as possible, at all events in the form in which it was promulgated.

It has been pointed out by Professor Osborn that in the palæontological record it is found that the points of greatest wear in the molars of more ancient forms are just the places in which in succeeding periods of time new cusps appear.

Granting the inheritance of acquired characters, this seems more easy to follow. We know as a perfectly familiar fact that the stimulus of excessive wear, conveyed probably through the dentinal fibre, does stimulate the corresponding odontoblasts to increased action, and that new dentine is built on to the wall of the pulp cavity to thicken it at the threatened point.

To the mind of the Neo-Lamarckian it would not be a long step from this to the earlier and stronger development of dentine at this point in a succeeding generation, *i.e.*, to the development of a new cusp.

But if we accept this idea, then we are confronted with a difficulty in that Cope's view of the plastic yielding, if it may be so expressed, and Osborn's idea of a reaction leading to an increased resistance, seem contradictory, as they would both arise as a consequence of forces not very different acting upon a tooth.

Moreover, Cope's idea seems to involve a greater degree of fixity in the attachment of the teeth than practical experience finds to obtain. For a tooth quickly yields to a constant or frequently recurrent pressure in any lateral direction especially, so that one would expect the teeth of the ruminant to move in their sockets rather than to be affected in form. Cope himself recognises this as a factor which has determined the outward leaning of the incisor teeth of the lemurs, which appear to use their front teeth to comb out their fur.

If we are to accept in any form the idea of kinetogenesis, may it not be that the teeth have undergone some complete lateral displacement, and that this has been met by the endeavour, so to speak, of the teeth to resume the upright position by a growth back towards the middle line of those parts of the tooth which lay between the points of impact.

Dr. Wortman extends the idea of kinetogenesis yet further, thinking that the cingulum may be a wrinkle or fold produced by long continued pressure applied vertically, and that division of single roots into two may have resulted from a backward and forward rocking of the tooth in mastication.

Cope thus formulates the influences which he conceives to be the most important :—

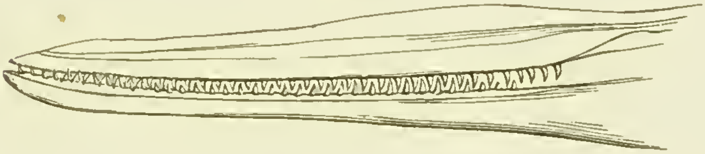
1. Increase of size of a tooth, or of a part of a tooth, is due to increased use, within a certain maximum of capacity for increased nutrition.

2. The change of direction and use of a tooth take place away from the direction of greatest, and in the direction of least resistance.

3. It follows from their greater flexibility, that the crests or crowns of teeth yield to strains more readily than do the cusps.

4. The increase in the length of crests and cusps in all directions, and therefore the plications of the same, is directly as the irritation from use to which their apices and edges are subjected, up to the limit set by the destructive effects of such use, or by the recuperative energy of nutrition.

FIG. 146 (¹).



5. The direction of growth of the branches of a **V**, or of the horns of a crescent, will be in the direction of movement of the corresponding parts of the opposite jaw.

The process of evolution being a progress from the simple to the complex, an acceleration or hypertrophy of some parts eminently useful, and a retardation or dwindling of those which are becoming less evertical, some naturalists have sought to generalise and to trace out the history of mammalian teeth from simple conical forms, such as are to be met with in homodont cetacea.

We have learned that, with some exceptions, the teeth of fish and of reptiles are alike in all parts of the mouth, but this only occurs in a few mammalian groups, and it also happens that this simplicity goes hand in hand with the

(¹) Jaw of common dolphin.

absence of any functional succession in the teeth. Hence Homodont and Monophydont are terms often applicable to the same creatures. Of Homodont mammals, *i.e.*, those which have similar teeth in all parts of the jaws, the Cetacea afford good examples. Thus the Dolphin (see Fig. 146) has a great number of sharp conical teeth, those of the lower jaw alternating with and fitting in between those of the upper jaw, and it is suggested that the teeth of higher mammals are derived from some such a dentition, though not from these particular ones, for they do not stand in the line of descent, but have retrograded so far as teeth go. It is suggested by Kükenthal and Röse, though the idea is much older than their time, that the occurrence of multicuspid teeth may be explained by the shortening of the jaw and consequent crowding of the teeth leading to the coalescence of several simple conical teeth to form a single tooth with several cusps; thus they would regard the five-cusped human molars as derived from the coalescence into one tooth of five originally distinct simple conical teeth. This view is supported by Virchow, who thinks that in a case in which the place of a molar had been taken by three peg-shaped denticles with separate roots, these are evidences of atavism; multicuspid teeth having been arrived at by the fusion of several originally separate teeth of a homodont dentition, they would regard any five-cusped human lower molar as the descendant of five originally distinct simple cones.

But a study of the palæontological record negatives this idea, for if it were at all true we should have to account for the phenomenon of the fused tooth again becoming simpler in Mesozoic mammals, and then again at a later period becoming furnished with more numerous cusps, which does not commend itself as probable.

It would appear to be highly probable that were the geological record tolerably complete, linking forms would be found which would reduce to insignificance the differences that existed between allied creatures in respect of their dentitions, and then we should be able to point to one unbroken series of dentitions, beginning from the most highly generalised forms, and terminating in the most extreme modifications known to us. But a good idea of the imperfection of the record may be gathered from a review of the earliest mammals which have been discovered.

The earliest mammalian dentitions known to us carry us back no further than Mesozoic times, and of the Mesozoic mammals we may say that they had mostly smooth cerebral hemispheres, no inflection of the angle of the lower jaw, and forty-four or more teeth: of these the canines had two roots, and the premolars and molars were little differentiated from one another. The generalised members of these, whom Professor Marsh proposes to group under the new order Pantotheria, were perhaps the ancestors of the modern specialised Insectivora. ("American Journal of Science," April, 1887.)

The usual pattern of tooth was tricuspid, the central cusp greatly preponderating, but it remains uncertain whether these Mesozoic mammals were Marsupials or Placentals, or whether they may be generalised forms from which both have been subsequently derived.

Of the few mammals known to have existed in Mesozoic times, about a dozen genera have been got from a single locality, the Purbeck bone bed; this is a fresh water deposit found near to Swanage, and it is no larger than the floor of a very moderate-sized room, and only six inches deep. From it quite a number of forms have been described, some of which have several incisors, and a general insectivorous type of dentition (Polyprotodonts); others have a single long-pointed incisor on each side of the median line (Diprotodonts) like existing kangaroos, and compressed blade-shaped premolars, so that even at this period we are already far from generalised parent forms. From this tiny patch comes most of our record of English Mesozoic mammalia, and in it are forms so differentiated, as for example Plagiaulax, as to clearly indicate that at this date mammals had long existed and were present in the country in great numbers, yet we know nothing at all of them.

Recently a considerable number have been found in

Wyoming, in Jurassic formations, and Professor Marsh, pending evidence which would place them either amongst the Metatheria or Eutheria, proposes for them the provisional orders Pantotheria and Allotheria.

Marsh considers that his Pantotheria were probably placental, and his Allotheria, which had fewer teeth, mere specialisation of premolar and molar teeth, and an inflected angle to the lower jaw, were probably Marsupial mammals, but he infers from what is known of the earliest mammals that the placentals are not descended from the Marsupials, but that both have arisen from a common stock, perhaps of Monotreme character.

Those American Mesozoic mammals, known only by teeth and jaws, were very similar to the European forms.

The Amphitherium (lower jaw alone) is one of the earliest dentitions known, coming from the Jurassic formations: it had sixteen teeth, which, so far as their forms can tell us, were

$$\mathrm{i}\,\frac{-}{3}\;\mathrm{c}\,\frac{-}{1}\;\mathrm{pm}\,\frac{-}{6}\;\mathrm{m}\,\frac{-}{6}.$$

Of Mesozoic mammals in general it may be said that the earliest are known by isolated jaws, or even by a few detached teeth, but those coming a little later are better known, largely by the magnificent finds which have rewarded the American naturalists.

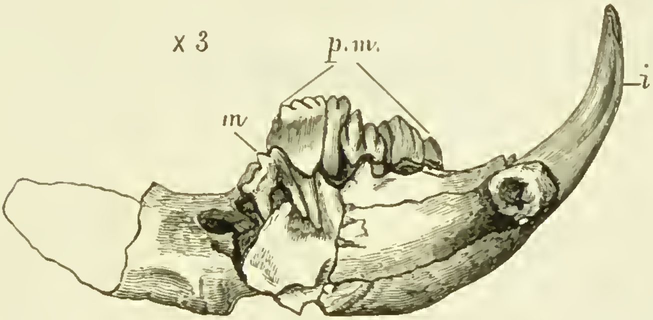
A large series of early mammals have come from the Puerco beds of New Mexico, which are either Eocene Tertiary, or even a little earlier. (Osborn and Earle, "Bullet. Americ. Mus. Nat. History," 1895.) They are remarkable for the large number of orders represented, from the Multituberculate allies of Plagiaulax to representatives of the Primates, which appear already to have been both abundant and specialised.

The so-called Multituberculata, so named because of the many tubercles which their molar teeth present, appeared in Mesozoic times and extended on into the Puerco beds.

They may be provisionally divided into two groups, one of which includes Polymastodon and its allies, and the other comprises Plagiaulax and allied forms; it must not be inferred that they were necessarily marsupials, indeed, some writers consider them to have possibly been Monotremes.

Professor Marsh has described several Mesozoic forms like Plagiaulax, but upper and lower jaws not having been found together *in situ* it is somewhat problematical which upper belongs to which lower jaw.

FIG. 147 (¹).



The lower jaw of one of these, to which the name Ctenacodon has been given, found in strata of Jurassic age, has a single long pointed incisor, four compressed cutting premolars, and two minute tubercular molars behind them.

This is so strongly differentiated that it cannot be regarded as an ancestral type, and the manner of succession reminds us of that seen in Marsupials; the Plagiaulacidæ have compressed cutting premolars resembling somewhat those of Hypsiprymnus. A great controversy once raged as to the probable diet of these forms.

Professor Owen, basing his arguments largely upon the presence of premolars which possessed elongated and sharp-edged blades, held that Plagiaulax was carnivorous, saying that it possessed an effective dental machinery for predatory life; Dr. Falconer and Sir W. Flower have shown this

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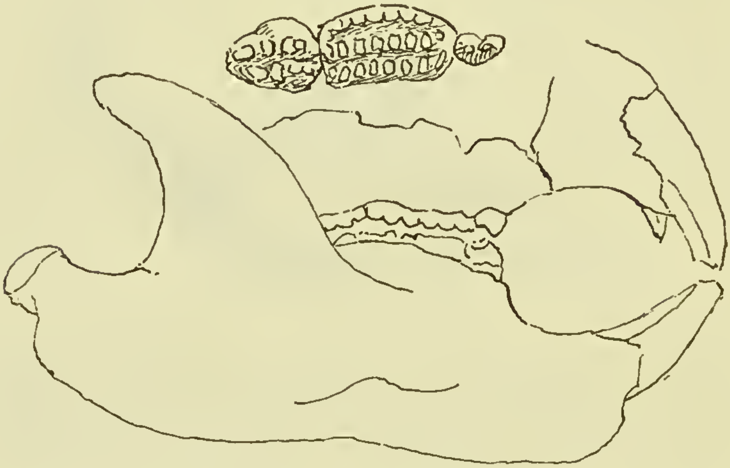
(¹) Lower jaw of Ctenacodon. (After Marsh.)

view to be untenable, or at least unsupported by adequate evidence.

Professor Marsh remarks that all the mammals older than Tertiary times may have been Insectivorous, but that Plagiaulax shows an adaptation to some special food, whether animal or vegetable is as yet unknown.

The true molars do not, however, resemble those of existing marsupials; on the other hand, the angle of the lower jaw is inflected as in them.

FIG. 148 (¹).



Polymastodon (Cope), besides being possessed of multituberculate molars (there are no less than twenty-eight oval cusps upon the first upper molar), had two long slender incisors in both upper and lower jaws, with the enamel confined to the anterior surface; in the upper jaw there were in addition two small additional incisors. In the lower molars there were normally only two rows of cusps, though occasionally signs of an additional row are present.

The other prevalent type of Mesozoic mammals resembles somewhat the polyprotodont marsupials; there are three or more lower incisors, the canines are pronounced, and

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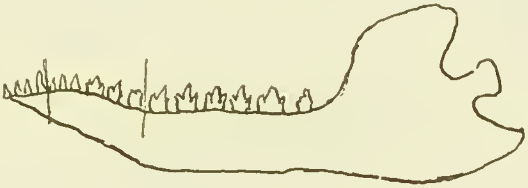
(¹) Dentition of Polymastodon. (After Osborn.) The grinding surfaces of the multituberculate upper molars are shown separately.

the cheek teeth are cuspidate, reaching in some cases the number of twelve.

The cusp pattern of the molars varies between a simple cone, a cone with additional subsidiary cones at the front and the back, a triconodont type, and the full tritubercular type.

Associated with the tritubercular teeth is also always a pentadactyle foot. There is a difficulty in determining which are to be called premolars and which molars, but the resemblance of certain Insectivorous teeth, *e.g.*, those of Chrysochloris, to the primitive tritubercular tooth, as well as certain other characters, make some naturalists insist upon the affinity of these mammals with the Insectivora. Their characters are generalised, and the typical mammalian formula is of frequent occurrence.

FIG. 149 (1).



Such being the earliest mammals known to us, Professors Cope and Osborn have evolved from the study of them a theory of the genesis of tooth forms, which has gained some considerable acceptance. They find that in the very generalised form, Dromatherium, the teeth are little more than simple cones; in Amphilestes they find a triconodont stage; while in Spalacotherium the three cones instead of being placed in a line, have become placed in the upper teeth as two outer and one inner cusps, and in the lower as one outer and two inner cusps.

At this stage we have what is termed the tritubercular tooth, which with slight modification is exceedingly common in the mammals of the early geological periods.

(1) Lower jaw of Amphilestes, from the Stonesfield slate, × 2. (After Owen.)

In order to give precision to the further study of tooth forms, special names have been given to each of these primitive cones or cusps; thus the original principal cone is called the protocone, and of the two subsidiary cones, the anterior one is called paracone, and the posterior one metacone. The corresponding lower tooth cusps are distinguished by being called protoconid, paraconid, and metaconid. Thus the corresponding cusps are inner (protocone) in the upper and outer (protoconid) in the lower teeth, corresponding to the original single cusps; the antero-external of the upper, and the antero-internal of the lower jaws being called paracone and paraconid respectively; and the postero-external of the

Fig. 150 (1).

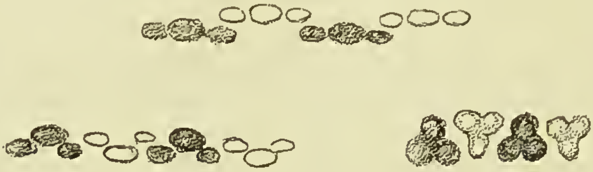
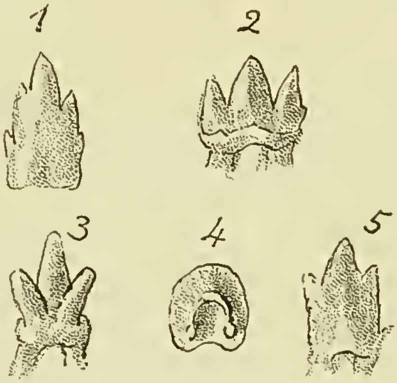


Fig. 151 (2).



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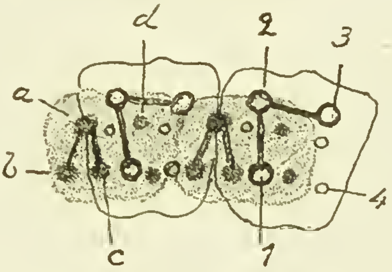
(1) Diagram (after Cope) of upper (shaded) and lower (clear) teeth. Triconodon. Menacodon. The ideal tritubercular teeth, approached by Menacodon.

(2) 1. Tooth of Dromatherium. 2. Triconodon. 3. Tooth of Spalacotherium (tritubercular) inner aspect. 4. Working surface. 5. Outer aspect. (After Osborn.)

upper and the postero-internal of the lower primitive triangle the metacone and metaconid respectively.

Thus, in the earliest type, the upper and lower teeth are alike, the cusps being arranged in line; and in the simple tritubercular type they are still alike, save that the apex of the triangle is directed outwards in the lower, and inwards in the upper jaws (ex. Spalacotherium, and? Chrysochloris); then, whilst the primitive triangle still remains the chief part of the crown, other cusps come to be added; for instance, a posterior heel carrying a cusp termed the hypoconid or hypocone, as the case may be, this stage being termed the trituberculo-sectorial type; and very often this added heel carries two cusps, one inner and the other outer, making a quinque-cuspid tooth, such as is represented in the above figure, which is adapted from Professor Osborn.

Fig. 152 (¹).



In this figure the teeth are looked at from below, the lower teeth (shaded) being supposed to be transparent so as to show the relation of the cusps of the upper and lower teeth to one another. The cusps of the lower teeth, which belong to the primitive triangle, are black and of larger size than those added; those of the upper triangle are ringed, and also of larger size than those added; the cusps of the lower

(¹) Diagram of two upper and two lower quadri-tubercular molars, adapted from Osborn in order to show relation of cusps. The shaded lower molars are supposed to be transparent, and to be looked at from below. The cusps of the primitive triangle are marked heavily, and are united by strong lines, those of the lower being solid, those of the upper ringed. *a.* Protoconid. *b.* Paraconid. *c.* Metaconid. *d.* Hypoconid. 1. Protocone. 2. Paracone. 3. Metacone. 4. Hypocone.

teeth are indicated by letters, those of the upper by numbers. Of the additional cusps, the hypocone and hypoconid are numbered 4 and lettered *d*; the fifth cusp or entaconid is not lettered at all, for the sake of clearness in the diagram, but in the upper tooth its homologies are not quite clear, there often being two corresponding additions, making six in all. These are called protoconule and metaconule, and are represented in the diagram by the smaller unnumbered rings. The cusps of the primitive triangle are often joined by ridges.

The formation of the quadri-tubercular tooth is got at, not by the simple addition of one cusp to the primitive triangle, but by the addition of two and the more or less complete suppression of one of the three of the primitive triangle.

It will be seen that in the case of the lower tooth the hypoconid is added, making a quadri-tuberculate tooth, and then the entaconid making a quinque-tuberculate tooth, but in the upper tooth a quinque-tuberculate tooth is got by the occurrence of two intermediate cusps, not numbered in the figure, the protoconule and metaconule ; whilst the final addition of the hypocone makes a six-cusped tooth ; there is thus a slight want of sequence in the order in which the cusps come upon the scene in the upper and lower teeth, which makes their correspondence open to question ; indeed, it is fully admitted by Osborn that there are doubts as to the homologies of these secondary cusps in the upper and lower teeth. To further illustrate the application of this nomenclature, taking the lower teeth, the lower carnassial tooth of the carnivora has the primitive triangle, with connecting ridges and an additional low hypocone. The same type occurs in many marsupials and insectivores.

Add the hypoconid and entaconid to the primitive triangle, and we have a common type of quinque-tuberculate molar ; then suppress one of the cusps of the triangle (the metaconid in Carnivora or the paraconid in Ungulata), and we get the quadricuspid bunodont molar. But the reader who wishes to follow these transformations in detail must be referred to the original memoirs.

LOWER MOLARS.

CUSPS.

Primitive Triangle.
Antero-external = protoconid.
Antero-internal = paraconid.
Intermediate (or after the loss of the paraconid antero-internal) = metaconid.
Postero-external = hypoconid.
Postero-internal = entaconid.

UPPER MOLARS.

Primitive Triangle.
Antero-internal = protocone.
Antero-external = paracone.
Postero-external = metacone.
Postero-internal (sixth cusp) = hypocone.
Antero-intermediate = protoconule.
Postero-intermediate between metacone and hypocone = metaconule.

As has been already mentioned, this occurrence of a trituberculate molar is said to have been almost as universal amongst Mesozoic mammals as a pentadactyle foot, the whole triangle of the lower tooth in closure of the mouth passing in front of that of the upper, the teeth of the two jaws thus alternating, rather than meeting grinding surface to grinding surface. Professor Osborn believes that these three primary cusps formed a central stage from which the great majority of recent molar types have diverged by the addition, modification, and reduction of cusps; we must except the Monotremes, the Edentates, and possibly the Cetaceans, although there is considerable evidence that the Cetacean molars were once of a triconodont type.

It is very interesting to note that even when teeth have become flat-topped and quadri- or quinque-tuberculate, the primary triangles of the upper and lower teeth retain their old relative positions alternate with one another. (See diagrams on pp. 332 and 333.)

The stages of tritubereulism, a term first employed by Rutimeyer, are thus set forth by Osborn :—

I. Haplodont Type.—A simple conical crown, with single root, not well marked off from the crown. Not as yet known among primitive mammalia.

I a. Protodont Type.—One main cone with lateral accessory cuspules; root grooved. Ex. Dromatherium from American Trias.

II. Triconodont Type.—One central cone with two lateral accessory cones; root double. Ex. Triconodon.

III. Tritubercular Type.—Crown triangular with three main cusps, the central or principal cone internal in upper molar and external in lower molar. Ex. Spalacotherium and Asthenodon.

In various sub-types the primitive triangles form the main body of the crown, to which other secondary cusps are added. They diverge towards bunodont teeth, in which a quadri-tubercular form is assumed by the loss of one of the primary cusps and the addition of a heel which contains two secondary cusps, and towards a sectorial type in which the heel is low, and the three primary cusps are connected by cutting ridges.

Such is in brief the doctrine of trituberculism, the terminology of which has gained currency in most recent literature. And for the present the determination of the homologies of the cusps set forth by Osborn seems to hold the field, though it may come to be modified in the future; for this reason, in the later part of this book, little or no attempt has been made to give these homologies in describing the teeth of individual mammals, for as yet the doctrine has not gained universal acceptance and there are difficulties of some weight in the way of its application.

Thus authorities differ in the determination of the homologies of the cusps. There are those who dissent from the proposition that the protocone is on the inside in the upper teeth, holding that it is on the outside in both upper and lower teeth; again, Scott ("Proceedings of the National Academy of Sciences, Philadelphia," 1893) considers that it is not true of premolars, though he accepts it for molars, claiming that even where the premolars attain to a close resemblance or identity with the molars, yet the resemblance is superficial, and that it has been got by a different process, the protocone in them being on the outside in both jaws.

He proposes for the premolars a slightly different nomenclature, namely, protocone, deuterocone, tritocone, tetracone, in the order of their successive appearances in the palæontological series. If this could always be ascertained, this nomenclature would seem an improvement, but time alone will show which will establish itself in general use. In the paper referred to, he applies it only to the premolars, but it is undesirable to multiply terms if it can be avoided.

He considers that the internal cusps of premolars have been derived from elevations of the cingulum, and not from any ancestral tritubercular cusp. To this view Cope lends some support, remarking that we "seem to have here an excellent illustration of the origin of two identical structures by different evolutionary routes," rather than regarding it as a difficulty in the acceptance of the theory generally.

It is also questioned by Dr. Forsyth Major, who points out that the very earliest mammals known to us were not tritubercular, but multitubercular, and hence that we have just as much ground for supposing that the tritubercular molar, when it does occur, has been arrived at by a process of reduction in cusps, as that it is derived from the triconodont type.

Another stumbling block has been pointed out by Dr. Marett Tims. ("Trans. Linnæan Soc.," Vol. XXV.) It would be in accordance with other facts in development if the primitive cusp, even though in the adult it was reduced in size below the others, should be the first to appear in the course of development. But it happens that neither in Primates, Marsupials, nor Canidæ, does it do so; the protoconid does, but the protocone does not: and in some it is even not the second to appear, the metacone as well as the paracone appearing in the tooth germ before it. Goodrich has further pointed out that there is no record known to us of the beginnings of the change from the triconodont stage to the tritubercular.

We may safely say that the earliest mammals, known only by the jaws, were perhaps monotremes, but at all events they were so modified that they do not stand in the direct line of descent, and their molars were multituberculate.

Then in Mesozoic times we find a few simpler forms, but some were haplodont, more were triconodont, and by far the greater number were trituberculate. And here we are upon assured ground, for every known Triassic, Jurassic, Cretaceous and early Eocene mammal is in some stage of Trituberculism or of Multituberculism.

No bunodont forms occur in the Mesozoic period, but they come in in the Cretaceous period. The early and very general assumption of the tritubercular type indicates that the simpler forms are to be sought outside the mammalia, and it suggests that where we find it in mammals it might be due to retrogression.

Whatever may be the precise homologies of the cusps, from these trituberculate types of tooth are probably derived the more complex pattern of the teeth of later mammals.

Then we have the suppression of cusps, of entire teeth, or even of the one or other entire set of teeth; and in a few we have dentitions in which, in the adult, the persistent teeth perhaps belong partly to the one and partly to the other set.

Thus the evidence points to a unity of ancestry for monotremes, marsupials and placental mammals, but it equally shows that they diverged along three lines, and are not by any means in one line of descent.

Besides the introduction of new cusps, the pattern of a tooth may be complicated by infoldings of its surface, whether on its sides or on its apex.

If we take a simple conical tooth with one cusp, such as a canine, and grind or wear down its apex till the terminal portion of enamel is removed, its blunted end will present a more or less circular area of dentine, surrounded by a rim of enamel. If we imagine a tooth with four long similar cusps, we shall at a certain stage of wear have four such areas, while eventually, as the tooth gets worn down below the level of the bases of the cusps, there will come to be a single larger area of dentine surrounded by enamel. Thus in those teeth the grinding surfaces of which are rendered complex in pattern by the presence of several cusps, the pattern changes from time to time as the tooth wears down; while the addition of thick cementum filling up the interspaces of the cusps, adds a further element of complexity, as is seen in the teeth of most herbivorous creatures. The change of pattern induced by the wearing down of the surface to a lower level is well and simply illustrated by the "mark" of the incisor teeth of a horse.

Fig. 153 (1).

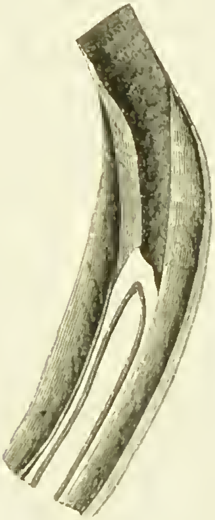
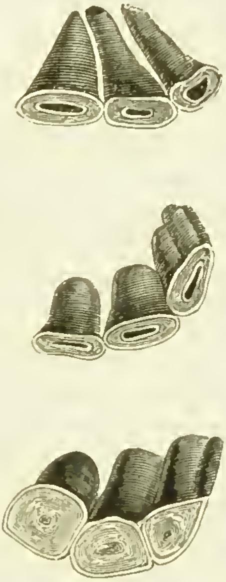


Fig. 154 (2).



In an uncut, and therefore perfectly unworn tooth, the condition of the apex may be compared to the finger of a glove, the tip of which has been pushed in or invaginated.

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(1) Horse incisor, longitudinal section.

(2) Horse incisor, showing the mark at various ages.

The depression so formed is, like the rest of the surface, coated with enamel, and with a thin layer of cementum.

When the tooth is worn down to a considerable extent, we have a field of dentine, in the centre of which is an oval ring of enamel: within this a space filled with the *débris* of food, &c. This constitutes the mark, and as the tooth becomes further worn down, below the level of the bottom of the pit, the mark disappears, and a plain area of dentine results.

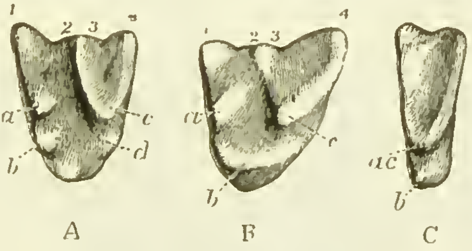
Somewhat similar inflections occur abundantly also upon the sides of teeth. The inflection of the surface, which in the incisors of the horse is of the simplest possible form, may be cruciform, or variously waved and broken up, thus leading to all sorts of complications of surface. As the tooth becomes worn, the longitudinal inflections, running in from the sides, may also be oblique, or variously waved, or they may extend through the entire width of the tooth, thus cutting it into a series of plates of dentine and enamel, fused into one tooth by the cementum. (See Fig. 159.)

Without wearying the reader by fully tracing out the genesis of each cusp, mention may be made of a very instructive series of comparisons of the molar teeth of Insectivora by Mr. Mivart ("Journal of Anat. and Physiol.," 1868), pointing out that within the limits of this group a great variety of patterns is met with, the several modifications being connected by transitional forms. A V-shaped tooth of tritubercular aspect occurs in some of the Insectivora of Madagascar and Africa, while in many others there is a more complex or W-shaped pattern.

Often upon the molar teeth (upper) of Insectivora there are four principal cusps (lettered *a*, *b*, *c*, *d*, in the figure) which are more or less connected by ridges; such simple teeth are met with in the elephant mice (Macroscelides) and the hedgehog. The cingulum is well developed in most of the group, and the further complexity of the crowns, which often bristle with sharp points, seems brought about by the elevation of the cingulum into long sharp points, equalling, or exceeding in length, the principal cusps of the tooth.

Thus in Urotrichus, a Japanese creature having affinities with the mole, the external cingulum is elevated into three distinct pointed cusps, united by ridges with the two principal cusps, an arrangement which gives a sort of W pattern to the surface, while to the inner side the cingulum forms another cusp, so that there are in all eight cusps; the common mole has the third cusp developed from the outer cingulum, but its two inner principal cusps are fused together and lose their distinctiveness. The suppression and fusion of cusps is carried to a much greater extent in the compressed teeth of the iridescent mole (Chrysochloris), but there are intermediate forms which render it easy to identify its reduced parts with those corresponding to them in the mole or in Urotrichus.

Fig. 155 (1).



Speaking generally, it may be said that new cusps are added to the number already existing, by the cingulum becoming elevated into points; it is not very unusual to see subsidiary cusps obviously originating in this way upon human molars.

Ridges may variously connect the cusps; Mivart suggests that the coalescence of two or more cusps to form an exceedingly elevated point is illustrated by the carnassial tooth of Carnivora; to this transformation certain marsupial teeth form the clue, as they afford unquestionable evidence of such coalescence by a gradational series of small modifications in this direction occurring in allied creatures. But this view is at variance with that of Cope and Osborn. Whilst Mivart regarded the simple tritubercular tooth as derived by compression and fusion of cusps from the others, they would advocate a course of modification the converse of this.

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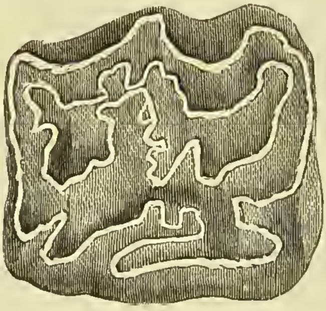
(1) Upper molar teeth of (A) Urotrichus; (B) Mole (Talpa); (C) Chrysochloris (the Cape iridescent mole). The four principal cusps (Mivart) are lettered *a*, *b*, *c*, *d*, the others being elevations of the cingulum of secondary importance. Woodward suggests that their homologies are: *a*. Paracone. *b*. Protocone. *c*. Metacone. *d*. Hypocone.

A common pattern of tooth is formed by the junction of the two anterior and two posterior cusps by simple ridges; and the cingulum may connect the outer ends of these two ridges; such a tooth is seen in the Tapir, and in the Palæotherium. By the varied obliquity of these ridges, and by the introduction of secondary inflections, patterns apparently dissimilar are arrived at.

Fig. 156 (1).



In the molar teeth of the horse, arrived at by a modification of the Palæotherium type, we have a surface constantly kept rough by the varying hardness of its different constituents.

In a worn tooth, we have upon a general field of dentine two islands of cementum, bounded by tortuous lines of enamel, and on the inner side a sort of promontory of dentine, bounded by enamel. The tortuous lines of enamel by virtue of their hardness will, at all stages of wear, be more prominent than the dentine or the cementum, and will hence maintain the efficiency of teeth as grinders.

The patterns of grinding surface thus produced are very constant for allied species, so that an individual tooth of a herbivore may sometimes be correctly referred to its genus, and always to its family.

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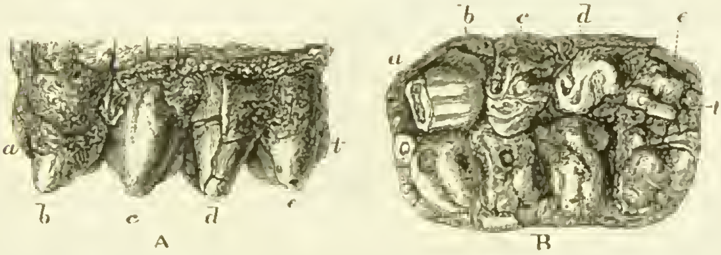
(1) Molar tooth of horse, showing the characteristic pattern of its grinding surface.

But as it will be necessary to recur to this subject from time to time, it will suffice for the present to point out that such correspondences do exist, and that all the complexities of pattern found, may, in practice, be reduced to some few types.

The development of additional cusps from up-growths of the cingulum, and the suppression or fusion of pre-existing cusps, may be traced by a comparison of the teeth of allied animals, and thus connecting links are found between patterns at first sight very dissimilar. The order Proboscidea affords, however, so instructive an instance of the manner in which an exceedingly complex tooth has been derived from a simple one, that it may be mentioned in this place as an example.

Fig. 157 (¹).



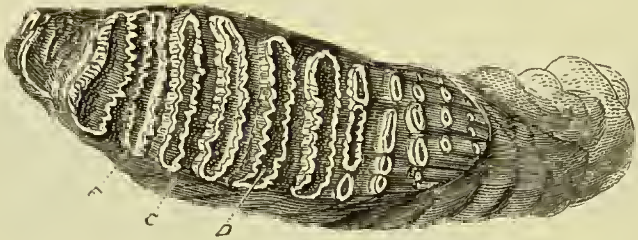
The tooth of the elephant is so strikingly unlike other teeth, that it might at first sight be supposed that it is more essentially different than is really the case. The clue to its nature is afforded by the teeth of an extinct Proboscidian, the Mastodon. If we take as our starting point the second true molar of one of the Mastodons (Tetralophodon)

(¹) Second upper molar of Mastodon (longirostris), from Falconer. About one-eighth natural size. The four transverse ridges, *b*, *c*, *d*, *e*, are seen to be, to some extent, divided into outer and inner divisions by a longitudinal cleft, much less deep than the transverse indentation. At the front there is a slight elevation of cingulum into a "talon" (*a*), and a similar one at the back of the teeth; by its further elevation additional ridges or cusps would be formed.

we find its crown to be made up of four strongly pronounced transverse ridges, the summits of which are made up of rounded eminences (whence the name Mastodon, from μαστος, a nipple). The four transverse ridges coalesce at their bases, and the crown is supported upon a number of roots corresponding to the ridges.

If we take the next tooth, or the third true molar, the general character remains the same, save that there are five ridges, and indications of as many roots; still the general correspondence of the ridges with the cusps of less aberrant teeth is obvious.

Fig. 158 (1).



The crown is coated by enamel, over which there is a thin layer of cement, which does not fill up the whole interval between the ridges.

Thus the tooth is not a very aberrant one; it is obviously nothing more than a tooth in which the somewhat numerous cusps are connected by transverse ridges, and are very long and strongly pronounced.

To convert the tooth of a mastodon into that of an elephant, we should have to multiply the number of ridges, to further increase their depth, to fill up solidly the interspaces between them with cementum, and to stunt the roots. The completed tooth of an elephant is a squarish or rather oblong mass, from the base of which spring contracted and stunted roots. It consists of a common pulp cavity, small in proportion to the bulk of the tooth, and

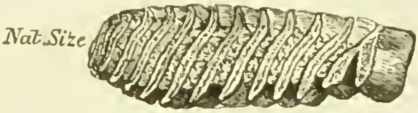
(1) Molar tooth of an Asiatic elephant, showing the transverse plates of dentine bordered by enamel.

deep down in the mass; from it many thin laminæ are sent up towards the surface, each forming the core of an area of dentine enclosed by enamel; and the interspaces of these exaggerated cusps are solidly filled in by cementum.

Between the Mastodon and the Indian Elephant are a number of transitional forms in which we are able to trace the gradual modification of the not excessively aberrant tooth of the Mastodon into the very peculiar huge molar of the Indian Elephant.

The numerous transverse plates of the elephant's grinders are united by dentine at their bases, and a common pulp cavity and truncated roots are formed; but in this last respect the molar teeth of the Capybara depart still farther from the ordinary type, for being molars of persistent growth, their numerous transverse plates of dentine and enamel do not become continuous, and there is no common pulp cavity. It is as though in an elephant's grinder the plates, which are for a long time distinct, never coalesced, but continued to grow on separately, being united with their fellows by cementum only.

FIG. 159 (¹).



Further differences may be due to the partial or complete absence of one or other of the constituent tissues.

In what might be termed a typical tooth we should have a single axial pulp cavity surrounded by hard dentine, this again being capped over the crown by enamel, and entirely invested by cementum.

The layer of coronal cement may be absent, as in Man or the Carnivora; or the investment with enamel may be only partial, as upon the front of a Rodent incisor, or on the tusk of a Pig or Hippopotamus; or a tooth may be composed solely

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(¹) Molar of Capybara, showing the transverse plates of dentine and enamel united to one another by cementum.

of a mass of hard unvascular dentine, coated with cementum, as in the tusk of an Elephant.

And just as endless varieties of teeth may be produced by the suppression, or partial suppression, of certain of the tissues, so differences may be brought about by the occurrence of other than the three usual tissues. Thus the remains of the central pulp cavity often becomes occupied by calcified pulp, forming "osteo-dentine;" this, which occurs in man as an almost pathological condition, is perfectly normal in many animals; in the sperm whale, for instance, or in the constantly growing teeth of the sloth, the central axes of which are occupied by dentine permeated by vascular canals.

CHAPTER XI.

THE HOMOLOGIES OF THE TEETH.

A superficial survey of the teeth of those mammals which possess two sets of teeth (Heterodont diphyodonts) will indicate that, notwithstanding the apparent anomalies brought about by adaptive modifications, a close correspondence between the several teeth of different animals exists. That is to say, we can generally identify incisors, premolars, and molars; nay, more, when an animal has less than the full typical number of a particular class of teeth, we can ordinarily say with certainty which of them it is that are absent.

Teeth are divided into incisors, canines, premolars, and molars, but these classes do not all admit of quite satisfactory definition. Incisors are defined as teeth implanted in the intermaxillary bone, a definition which has the merit of being precise; while on the whole there is a certain resemblance running through incisor teeth in most animals. But the definition of lower incisors as being the corresponding teeth in the lower jaw is a good deal less satisfactory, because they are not situate upon any distinct bone, and it has even been denied that there can be a true homology between a maxillary and a mandibular tooth.

Incisors usually have but a single root, but in Galeopithecus (erroneously called a flying Lemur) the outermost of the upper incisors are implanted by two roots, as is also the canine, which does not differ much from the incisors.

Molars are teeth at the back of the mouth, which come up behind the milk teeth (when there are any), and so have had no predecessors; they are generally subservient to grinding the food.

Premolars are teeth in front of the molars, usually differing from them by being more simple in form and being smaller, and, in typical Diphyodonts, by having displaced deciduous predecessors. But they are not always simpler in form, nor smaller (*e.g.*, in the horse), nor do they always displace deciduous predecessors (*e.g.*, they do not all do so in the Marsupials, and the first premolar but rarely displaces a deciduous predecessor in Mammalia), so that this definition is not absolutely precise. Still, as a matter of practice, it is usually easy to distinguish the premolars, and the division into premolars and molars is indispensable for the description of dentitions.

Any objection that can be raised to the name of premolar on the score of a short strictly logical definition being impossible, applies with tenfold force to the canines. (Cf. Messrs. Mosely and Lankester, "Journ. Anat. and Physiology," 1869.)

The nearest approach to a good definition is that which describes the canine as the next tooth behind the intermaxillary suture, provided it be not far behind it; and the lower canine as the tooth which closes in front of the upper canine.

A great deal of confusion has arisen out of the twofold sense in which the word "canine" is used: if it were always applied to the first tooth in the maxilla of the typical mammalian dentition quite irrespective of its size, &c., and to the lower tooth closing in front of it, no objection to its employment could be made, inasmuch as it would designate truly homologous organs.

But it so happens that the tooth in question is, in a very large number of familiar animals, developed to a large size and sharply pointed for use as a weapon, and so with the word canine there comes to be associated a teleological idea; and hence we are dissatisfied with calling the first maxillary tooth "canine," when there is some other tooth which is doing its special sort of work.

On the other hand, if we are to leave out of court all considerations as to size, purpose to which it is to be applied, and so forth, there is nothing left to make it deserving of a name distinguishing it from the four teeth behind it. So we must be content with some such statement as the following.

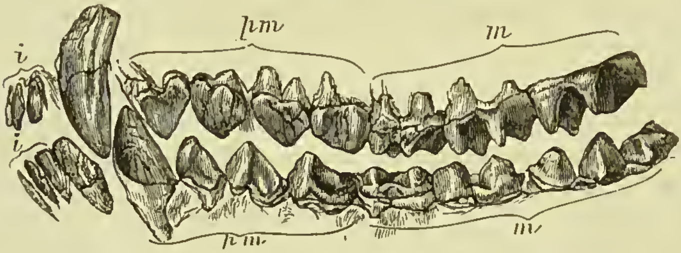
A very large number of animals, notably the Carnivora, have one tooth, situated a little way from the front of the mouth, developed to an unusual length and sharply pointed, for use as a weapon. The tooth which has undergone this adaptive modification is usually the first which lies in the maxillary bone; in fact, the foremost of the premolar series; but it occasionally happens that it is some other tooth which has undergone this modification. When we use the term canine we should generally mean a tooth so modified, and generally, but not always, should be alluding to the same tooth, *i.e.*, to the tooth which in the typical mammalian dentition comes next behind the outermost incisor—the first of the premolars, if we allow five premolars instead of four.

It would practically be very inconvenient to abolish the term canine, and some naturalists will continue to call the tooth which fulfils the function "canine," whilst others will apply the term to the homologous tooth, whatever be its shape; but it should be borne in mind that its significance is merely equivalent to "caniniform premolar," and thus that in describing the dog's dentition we should be less liable to be misinterpreted, were we to say that it has five premolars, of which the first is caniniform. To those who accept the doctrine of evolution it is not needful to say more, as it is hardly possible to resist the conclusion that the teeth of the parent forms were, like those of the present monophyodonts, not much differentiated from one another. Then, as animals diverged and became modified in accordance with their requirements, their teeth would become so far differentiated that they would admit of being classified. Thus the Carnivora would have attained to a stage of differentiation in which the canine is functionally certainly deserving of a distinction, whereas along other lines of descent, differentiation having not proceeded so far, or having proceeded in a somewhat different direction, it would not merit a distinctive appellation.

So it will be desirable to point out a few instances of the difficulties to which those anatomists are committed who call some tooth a "canine" in every case where a tooth is situated in the maxillary bone, close behind the suture which connects it with the intermaxillary bone, whether that or any other tooth be large and pointed, "caniniform" or not.

In typical Ruminants, the upper jaw lacks both incisors and canines (with certain exceptions), but in front of the lower jaw there are grouped together eight teeth, closely fitted together, and of almost exactly similar size and shape. The outermost pair of these teeth are called canines, because (i.) in some allied species the tooth in this situation is more pointed; (ii.) because this tooth shuts in advance of the upper canine when the mouth is closed (in those allied creatures which have an undoubted upper canine); (iii.) because it is cut later than the others (Owen); (iv.) because six is the typical number of mammalian incisors.

Fig. 160 (1).



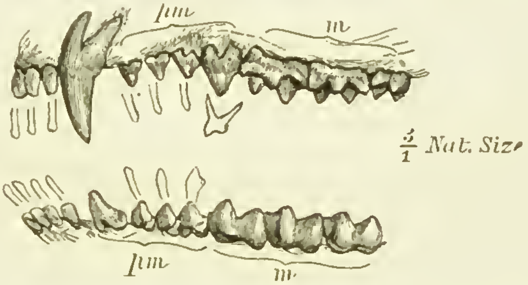
These three reasons are weak, because form (i.) is a very unsafe guide to homology, and as to the lateness of its development (iii.), it succeeds to the third incisor, by Professor Owen's own showing, after about the same lapse of time which separated the eruption of the second and third incisors.

Oreodon, an extinct Ruminant with caniniform teeth, has

(1) Oreodon Culbertsonii. (After Leidy.) It will be observed that in the upper jaw the four premolars of the typical mammalian dentition are behind the "canine," but that in the lower jaw the tooth which would fulfil the functions of a canine is the first of these four, and therefore is *not* the corresponding tooth to the "canine" in the upper jaw.

the eight incisors in the lower jaw in addition to a caniniform tooth, which is the fifth tooth counting from the front. With reference to the relative positions of the upper and lower teeth, determining which is and which is not "the canine" (ii.), no one, looking at the dentition of Oreodon, would be inclined to hesitate which teeth he shall call "canines;" yet the lower caniniform tooth shuts behind the upper, and therefore, according to this test, it is not a true canine.

FIG. 161 (1).



In the Lemurs there are similarly four or six procumbent teeth occupying the front of the lower jaw, of which the outermost pair are called canines, although not in the smallest degree meriting that name for any other reason than that they close in front of the caniniform tooth of the upper jaw, for they are just like the other incisors.

But it is in the *Insectivora*, which in some respects represent an ancient and generalised mammalian form, that the greatest difficulties occur.

To the mole no less than four dental formulæ have been assigned, all turning upon the identification of the canine. The difficulty is this: The upper tooth, which looks like a canine, has two roots, and is implanted (and its deciduous predecessors also lie—Spence Bate) within the limits of the

(1) Upper and lower teeth of the common mole. Spence Bate figured deciduous predecessors to all the incisors, canines and premolars, but Woodward finds no trace of succession in the first premolar, which he believes to be a persistent milk tooth. The milk tooth in the figure which lies over it is the deciduous canine.

premaxillary bone. With regard to this, Leche and Marsh point out that the canine is two-rooted in all the oldest known mammals, and that the reduction to one root goes hand in hand with the specialisation of its crown. Moreover, Leche does not attach much importance to its relation to the premaxillary bone, as he states that he is prepared to show that teeth rooted in the premaxilla in one species, and, therefore incisors, are to be found in allied animals rooted in the maxilla. And besides this, the lower tooth, which answers the purpose of, and looks like, a canine, closes behind instead of in front of the great upper teeth in other Insectivora.

Ericulus has a sharp, long, two-fanged tooth, in pattern of crown an enlarged premolar, in position of upper canine, and no caniniform tooth in lower jaw.

Centetes has typical canines, like a Carnivore.

Hemicentetes. The so-called canine, differs in no respect from the premolars behind it.

Erinaceus. So-called upper canine, two-rooted, and like the premolars which follow behind it.

Gymnura. Upper canine-like tooth has two roots ; a single-rooted lower pointed tooth closes in front of it.

Macroscelis and *Petrodromus.* The third or outermost incisor is two-rooted, long, and sharp, and plays the part of a canine.

Potamogale. A small tooth, in no respect different from the other premolars, is called a " canine."

Thus in some of the groups no tooth has been lengthened and pointed, so as to serve as a canine ; in others it is the wrong tooth, *i.e.*, not the same tooth as in the Carnivora, or as in other Insectivora. Consequently, in the Insectivora the elevation of a tooth into caniniform length and character is a mere adaptive modification, which may affect an incisor, or a premolar, or no tooth at all. Wortman states that though a premolar is often so modified, no example is known of a lower incisor becoming caniniform to oppose an upper canine.

As regards the other premolars, there is no difficulty in their determination in those dentitions in which all four milk molars are present, and are succeeded by permanent successors, but this by no means always happens. In a very large majority of cases, the first tooth behind the canine has had no predecessor and will have no successor; hence it remains uncertain whether it is a milk tooth which persists, or a permanent tooth which has had no representative in the milk series.

Woodward ("Proc. Zoolog. Soc.," 1896) discusses this question. pointing out that where there is no succession we may be dealing with a retarded member of an early or an accelerated member of a later set. In the Mole. in which there is no succession as regards this tooth, the enamel organ of pm_1 does not appear till after those of the milk teeth, but contemporaneously with that of pc. which tooth. however. appears long before any of the other permanent teeth. so that the date of the appearance of its enamel organ does not help much. He points out that in those cases amongst mammalia in which there is a succession. the canine is either vestigial as in Hyrax, or is widely separated from the next premolar as in Tapirus indicus. and further suggests that the usual suppression may be due to the great development of the canines. The first premolar is wanting or greatly reduced in all forms with great canines. and he thinks that the somewhat enlarged deciduous canine slightly stunts dpm_1, while the enormous permanent canine crowds out and totally suppresses ppm_1, so that he concludes by regarding the solitary pm_1 as really a persistent milk tooth (as dpm_1), a conclusion reached by Osborn on palæontological evidence.

The first premolar is apt to be very small, and it is remarkable that although it is usually almost functionless, it is apt to be long retained. Moreover, its eruption is apt to be later than that of the unquestionable second, third and fourth milk molars, so that it has some claim to be considered as a member of the second series in those cases in which no tooth change occurs.

But these difficulties which have been briefly pointed out do not prevent us from forming a pretty definite idea of what the usual complete mammalian dentition is, and for brevity it is usual to write this out in symbols, thus:—

$$i\,\frac{3}{3}\ c\,\frac{1}{1}\ pm\,\frac{4}{4}\ m\,\frac{3}{3} = 44.$$

This is what is styled a typical mammalian dentition, and when teeth are absent from it, we can usually say which are the absentees. And as it is not always the same tooth which is absent, a fuller dental formula may be written thus :—

$$\frac{i_1\ i_2\ i_3}{i_1\ i_2\ i_3}\ c\ \frac{1}{1}\ \frac{pm_1\ pm_2\ pm_3\ pm_4}{pm_1\ pm_2\ pm_3\ pm_4}\ \frac{m_1\ m_2\ m_3}{m_1\ m_2\ m_3},$$

$$\text{or}\quad i\ \frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3}\ c\ \frac{1}{1}\ pm\ \frac{1\,.\,2\,.\,3\,.\,4}{1\,.\,2\,.\,3\,.\,4}\ m\ \frac{1\,.\,2\,.\,3}{1\,.\,2\,.\,3}.$$

The general rule would appear to be that incisors were lost from the outer end, by the third being absent when there are only two incisors; premolars from the front of the series being the first to drop out of the formula, and molars from the hinder end, the third being the first to disappear.

But there are many exceptions to this rule—*e.g.*, the first incisor is the first to disappear in the otter, walrus, and some few others, and a question has been raised as to the homologies of man's two incisors.

When premolars are missing, it is said that they are lost from the front of the series. Thus in the Baboon the first and second premolars are absent, so that its dental formula written in full is :—

$$i\ \frac{1.2.0.0}{1.2.0.0}\ c\ \frac{1}{1}\ pm\ \frac{0.0.3.4}{0.0.3.4}\ m\ \frac{1.2.3}{1.2.3}.$$

This is generally true, but there are many exceptions, of which the following may be given.

In many bears the second premolar is often lost, as is also the third, but the first and the fourth are very constant; this is also true of some bats (1).

To make this more clear, Mr. Oldfield Thomas proposes to write out in full the dentition, thus :—

Bear :—

$$i\ \frac{1.2.3}{1.2.3}\ c\ \frac{1}{1}\ pm\ \frac{1.0.0.4}{1.0.0.4}\ m\ \frac{1.2.0}{1.2.3}.$$

There seems good reason to suppose that although modern marsupials have but three premolars, the original number was four, as in placental mammals. Thus in the extinct Triconodon, which was probably marsupial, Thomas has shown that all four premolars are present, and it is the last or fourth which alone shows vertical succession.

A study of the genus Phascologale, among the Dasyuridæ, in which pm_2 and pm_3 are very constant, but pm_4 variable down to being a minute and functionless tooth in one species, has shown that in Dasyurus, with its two premolars, it is pm_4 that has gone.

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(1) This is ascertained by the examination of allied forms, in which the third premolar is found to be so small as to be rudimentary.

And a comparison of many specimens, in one of which (Phascologale) four premolars were present, pm_2 being smaller than the others, and a skull of Dasyurus in which a rudimentary tooth was present between its two premolars, indicates that the other which has disappeared was pm_2.

$$\text{Thus Dasyurus has pm } \frac{1.0.3.0}{1.0.3.0},$$

$$\text{and Thylacinus pm } \frac{1.0.3.4}{1.0.3.4}.$$

Another difficulty arises from teeth which are beyond question of the permanent or replacing series, not persisting through the life of the animal, but being shed off.

The wart-hog is a conspicuous example of the early loss of teeth which clearly belong to the permanent series, all the teeth (premolar and molar) in front of the last great molar being cast off, and the dentition ultimately reduced to—

$$i\,\frac{2}{3}\;c\,\frac{1}{1}\;m\,\frac{1}{1}.$$

Amongst placental mammals the normal number of the molars is three.

The Tenrec, however, according to Mr. Oldfield Thomas, late in life cuts a small fourth true molar; this, coupled with its tritubercular pattern of molar teeth, indicates great antiquity. Of living mammals only the marsupials and Otocyon, a dog-like animal, have four true molars.

It is very unusual for the full typical number 44 to be exceeded: among recent placental mammals Otocyon alone exceeds, but some fossil Ungulates have more than the full number, and so have some marsupials.

Whether the parent forms of mammalia were homodont like the Cetacea or the Armadillo, or merely presented a much simpler and less differentiated series of teeth than recent mammals is still a matter of doubt, but if we could place in series all the mammals that have ever existed it would be impossible to determine the point at which a differentiation towards some specialised type could properly be said to commence, so gradual are the transitions in all cases in which they are pretty fully known to us.

THE MILK DENTITION.

Some forty years ago Professor Owen called attention to the fact that those mammals in whom the teeth situated in different parts of the mouth were alike in form (homodonts), developed only one set of teeth, and to indicate this characteristic he proposed for them the term "monophyodonts." Those which, on the contrary, had teeth of different size and form in various parts of the mouth (heterodonts), developed two sets of teeth; a "milk" set, which was displaced by a permanent set, and this peculiarity he expressed by the term "diphyodonts." As originally set forth, the terms homodont and monophyodont were interchangeable, for they designated the same groups of animals; in the same way heterodont was an equivalent for diphyodont.

But although this is true of a large number of animals if we take only functional teeth into account, there are even then exceptions to be noted.

Thus the nine-banded armadillo (Tatusia peba) is a true homodont; its teeth are all very nearly alike, they are simple in form, and they grow from persistent pulps. Yet it has been shown by Rapp, Gervais, and Sir William Flower, to have a well-developed set of milk teeth, retained until the animal is of nearly full size.

Thus it is a true diphyodont, at the same time that it is a true homodont mammal. But no milk dentition has been observed in the sloths, nor indeed at present has it been detected in other Armadillos, with the exception of a doubtfully distinct species, so that as far as functional teeth are concerned many homodont animals are monophyodont.

But recent researches have clearly shown that the term monophyodont is no longer of much use, for even in apparently monophyodont animals the tooth germs of another set of teeth, sometimes calcified a little, sometimes yet further reduced, have been found. Hence there hardly remains room for doubt that the primitive condition of mammalia was that of Diphyodontism, and that where only one set remains in full evidence, the other has been lost by a retrograde process, by the suppression of that which is not needed.

Upon the whole, our information respecting the "milk" or deciduous dentition remains still defective; but much light has been thrown upon the subject by the recent investigations of Kükenthal, Röse, Leche, Oldfield Thomas, Woodward, Marett Tims, Wilson and Hill, and others.

The perpetual replacement of teeth lost or shed in regular course, which characterises the dentition of fish and reptiles, finds no parallel in the case of mammals, none of whom develop more than two functional sets of teeth, though Leche believes that he has seen faint signs of a third series.

Just as homodont mammals as a rule develop but one functional set of teeth, so heterodont mammals as a rule develop two functional sets of teeth, though many exceptions to this rule also may be found.

The deciduous or milk set of teeth may be of any degree of completeness; the milk teeth in man answer the requirements of the child up to the age of seven years, and in the Ungulata they commonly remain until the animal has assumed its adult proportions. On the other hand, in many "diphyodont" animals the milk teeth disappear very early indeed, as in the mole (see Fig. 161); whilst there are many instances of the milk teeth being absorbed in utero. So that, in the extent to which the milk teeth are developed, the greatest variability is found to exist.

A perfectly typical milk dentition represents, upon a reduced scale, the adult dentition of the animal, with the exception only that sexual differences are but feebly marked, if indeed they are at all present. (See Fig. 162.)

Thus, as a general rule, the hindmost of the milk teeth bear more resemblance to the true molars which come up behind them, than they do to the premolars which come up from below to displace them, which latter are generally of simpler form.

In what may be termed the normal arrangement, each tooth of the milk series is vertically displaced by a tooth of the permanent series; but plenty of examples may be found of particular milk teeth which have no successors, and, on the contrary, of individual permanent teeth which have never had a deciduous predecessor.

Although the views advocated by him have become somewhat obsolete, the papers of Sir William Flower ("Journal of Anat. and Physiology," 1869, and "Trans. Odont. Soc.," 1871) remain valuable in giving an instructive series of comparative development of milk dentitions, and from them the accompanying illustrations are borrowed :—

FIG. 162 (1).

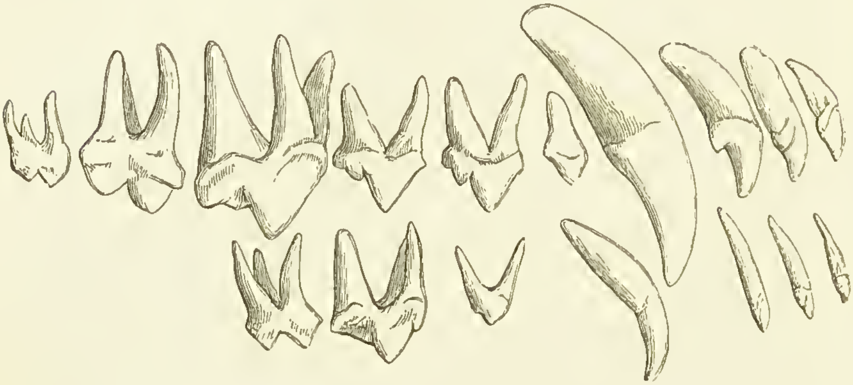
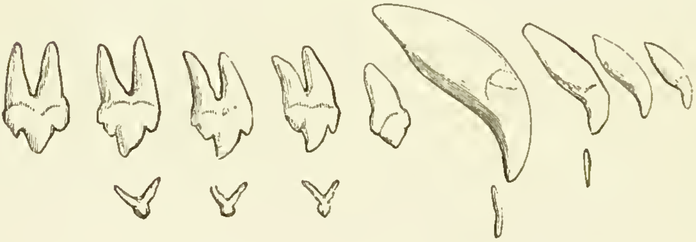


FIG. 163 (2).



Within the order Carnivora, the Dog and many others have a thoroughly well-developed set of milk teeth, which do service for some time; in the bear the milk teeth are relatively smaller, and are shed very early; in the seal the milk teeth are rudimentary and functionless, and are absorbed before birth, so that in the specimen figured the milk incisors had already disappeared.

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(1) Permanent and milk dentitions of a dog : the latter is well developed. Nat. size. (After Flower.)

(2) Permanent and milk dentition of a seal (Phoca Greenlandia). Nat. size.

FIG. 164 (1).

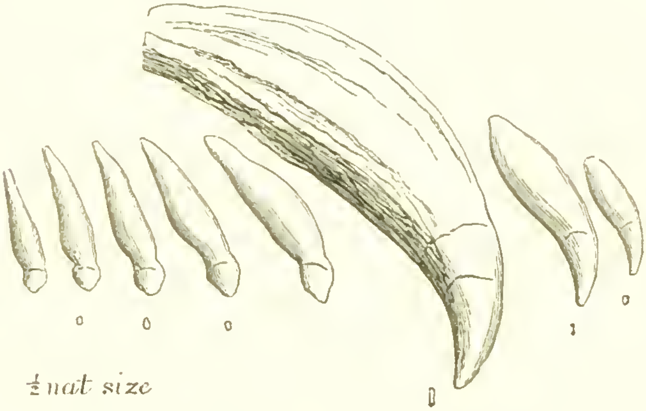
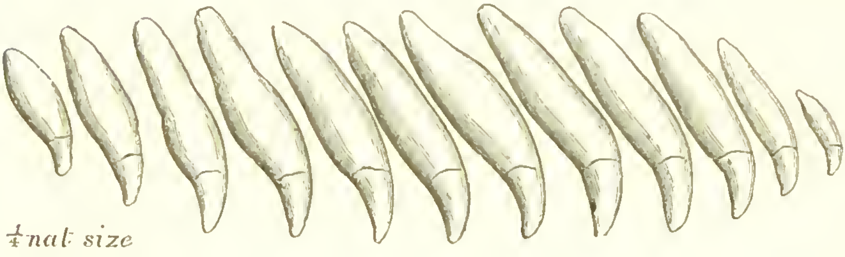


FIG. 165 (2).



In the elephant seal the milk teeth are yet more rudimentary, and the difference between its dentition and that of the monophyodont homodont Cetacean (Grampus) is not great; an observation which is the more interesting, inasmuch as this seal in other characters than its teeth approaches towards the cetacean group. From these facts, which are well indicated in the accompanying figures, Sir

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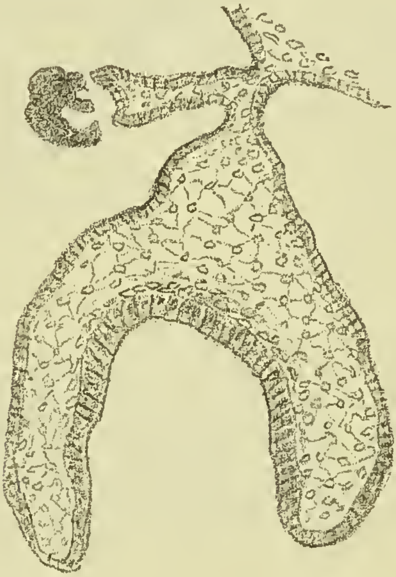
(1) Permanent and milk dentition of an elephant seal (Cystophora proboscidea).

(2) Teeth of the truly monophyodont grampus (Orca capensis). (These four figures are copied from Sir W. Flower's paper.)

William Flower argued that the permanent set of teeth of diphyodonts correspond to the single set of monophyodonts, so that the milk dentition, when it exists at all, would be something superadded.

This was a question upon which there was room for doubt, and although the facts adduced by Sir William Flower afforded the grounds for argument that this was the true interpretation, yet the known facts of development pointed the other way; and more recently the investigations carried out by means of complete series of serial sections of marsupial jaws by Kükenthal and Röse appeared to have rendered it almost untenable, so that Mr. Oldfield Thomas, at one time an adherent of that view, has now become a convert to the other, namely—that where only the one set exists, it is, in a large number of cases at all events, the milk set.

Fig. 166 (1).



But the question is still in abeyance, and turns largely, indeed wholly, upon the interpretation attached to more or less rudimentary tooth germs. The accompanying figure represents a stage of suppression in which although the enamel organ is but little differentiated, it is impossible to doubt that we have a true tooth germ, as an irregular calcification has taken place at its end. (Fig. 166.) But in a great number of outgrowths of the tooth band which have been regarded as representing tooth germs there is no such calcification to settle the question.

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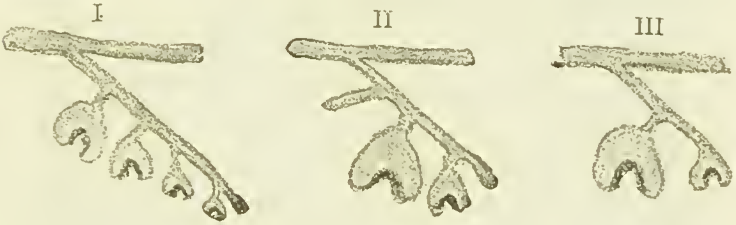
(1) Permanent tooth germ and aborted milk germ of the canine of a hedgehog. × 100. (After Woodward.)

The epithelial lamina (zahnleiste) descends into the mesoblastic tissue somewhat obliquely, inclining towards the tongue, and the buds which go on to form tooth germs appear upon its labial side at, or close to, its end for the time being. Consequently, as its free end goes on growing deeper into the tissues on the lingual side of the already forming tooth germs, we are justified in saying that any additional specialisation of the dental lamina which is situated on the lingual side of a formed germ belongs to a later generation of teeth, and conversely that any similar growth of the lamina which lies on the labial side of a formed tooth germ belongs to an antecedent generation.

FIG. 167 (¹).



Now, whilst in such a specimen as that figured on p. 241, we have in view at one time many generations of tooth germs, we do not find in mammals that more than two ever attain to functional development, and Fig. 167. III. represents what may be regarded as typical in the mammalia. Here we perceive that the germ of the successional tooth is at the end of the dental lamina—that it has, so to speak, used it all up, and that there is no prolongation beyond it. But this is not invariably the case; sometimes we may find a little prolongation of the dental lamina beyond and to the lingual side of the developing successional germs, and this is regarded by many writers as an indication of a post-permanent dentition

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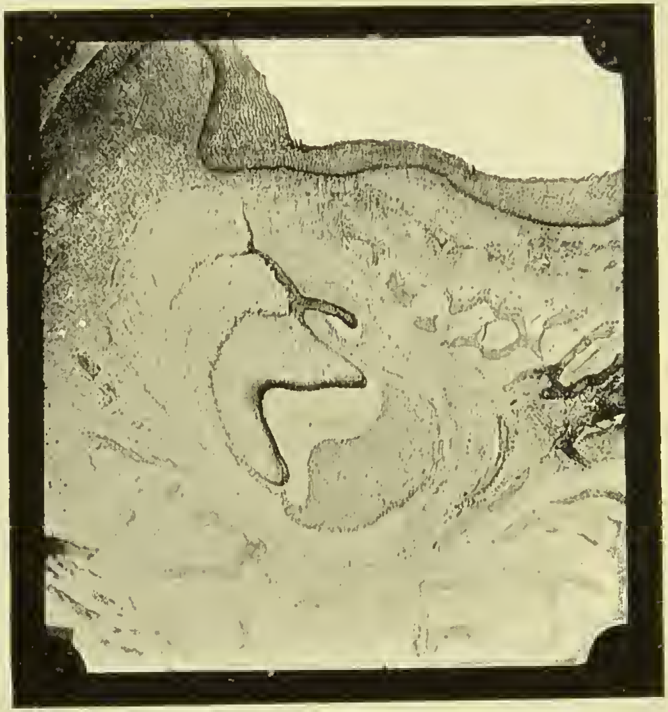
(¹) I. Diagram of indefinite succession in fish or reptiles. II. Diagram (hypothetical) of functional milk and permanent germs of mammalia, showing premilk and post-permanent rudiments. III. Diagram of typical mammalian succession, all tooth germs save the milk and permanent having totally disappeared. In all the diagrams germs which proceed to functional calcification are marked by darker shading.

in posse. Similarly we may find an outgrowth to the labial side of the milk tooth germ, and *à fortiori* of the successional germ, and this is nowadays sometimes interpreted as a vestigial premilk dentition.

But no one has, so far as I know, seen in any one specimen vestiges of all four at once ; had they done so they would, of course, have to be interpreted as premilk (vestigial), milk (functional), permanent (functional), and post-permanent (vestigial) (Fig. 176, II.).

As an example of the appearances which lead to diversities of interpretation the following figure may be given. In it the milk tooth germ is fully developed, and to its lingual side is the commencement of the germ of the successional tooth, both of these ultimately attaining to full functional development. But above the milk germ and to its labial side is an outgrowth of the tooth band, which, if it is to be regarded as an aborted tooth germ at all, must be referable to a premilk series. It is, however, not accepted as certainly representing a tooth germ by some who have studied this specimen.

FIG. 168 (¹).



Thus it may be objected that many outgrowths of a tooth band

(¹) Tooth germs of a pig, from a specimen lent to me by Dr. Marett Tims. The right is the lingual side of the specimen.

are not much differentiated, and that they are hardly worth calling tooth germs, even with the added qualification "vestigial." But it must be remembered that mammals are of great antiquity, and that we should not expect to find any highly-differentiated remains of long-lost structures.

In view of the hypotheses which are occupying so much of the attention of naturalists upon the relations of the two (or more) sets of mammalian teeth, it becomes important to decide how much differentiation of the epithelial lamina we shall be justified in regarding as adequate evidence of a tooth germ, but unfortunately there is no agreement on this fundamental point.

Kükenthal and Röse in particular, and following them a good many other writers, appear to be satisfied with remarkably little; almost any proliferation of the cells of the tooth band leading to its being thickened or "swollen," so that it is bud-shaped on section, is for them a reduced tooth germ; and Leche, whilst distinctly pointing out that neither a bud-shaped (as seen in section) enlargement of the band, nor even a connective tissue thickening about its free end can be held to establish it as a tooth germ, yet practically accepts as tooth germs a great many structures which show no more than this. It is true that such a swelling does take place where a tooth germ is about to be formed. It is true, also, that in certain cases we are able to trace a downward series from a well-marked and calcified tooth germ to ultimately nothing more than such a swelling; but it is also true that such swellings of the tooth band do take place beyond the second tooth germs of many mammals: and, in fact, in other positions where we have not the smallest ground for assuming that a tooth germ has ever existed beyond the evidence of the swollen lamina itself.

Hence, as is clearly pointed out by Messrs. Wilson and Hill ("Quart. Journ. Microscop. Science," 1897) mere enlargement of the tooth band, accompanied by some condensation of the mesoblastic tissue round it, is not adequate evidence. Of course, if it goes on to the bell-shaped cap with full differentiation of its outer and inner epithelia, and still more if there be the smallest calcification, no one will feel any scepticism.

But unfortunately a very large proportion of the supposed germs upon which speculation is rife, and upon which theories are freely built, are merely of this doubtful character.

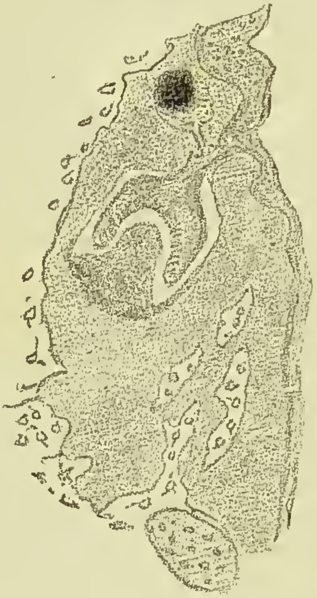
If we could find in any mammal all four sets of tooth germs going on to calcification, or even to such an amount of differentiation as would show that the outgrowths were really aborting tooth germs, all difficulty of interpretation would disappear; but unfortunately this is never the case. We do not find all four at once: neither are the supposed rudiments so far differentiated as to put their nature beyond all doubt.

So when we have to deal with what are apparently three sets of rudiments successional to one another, the question always has to be decided for the particular case, to which of the supposed four dentitions do the functional teeth of the individual belong, before we can assign a place to the extra rudiment, if, indeed, true tooth rudiment it be.

In the whole group of marsupials (with the exception of the Wombat) no tooth change had been demonstrated except in the case of an individual tooth, the last premolar, but here the vertical succession is curiously constant, though in the case of some of the Dasyuridæ it is shown in process of reduction and disappearance.

This succession of a single tooth had become established (in Triconodon) in very early geological times, and has been retained with remarkable constancy. Then came the researches of Kükenthal and Röse, who showed that the tooth band, beyond and to the lingual side of the germs of the functional marsupial teeth, becomes swollen, and as they gave to these enlargements the full significance of tooth germs (which has been denied them by Wilson and Hill) they regarded the dentition of marsupials as being a persistent milk dentition, with remaining rudiments of a suppressed (or first appearing ?) second dentition, a view which obtained a large amount of acceptance.

FIG. 169 (1).



But this interpretation of the functional teeth of marsupials rests upon the fact that supposed germs of a successional set—that is to say, germs upon the lingual side—of the developing teeth have been recognised in a considerable number of marsupials by Kükenthal. Leche, Woodward, Röse, and others, so that if we acknowledge these as tooth germs the functional teeth are certainly not the latest set represented by vestiges, and all probability would seem to be in favour of the view that the teeth of the marsupials really are persistent milk teeth.

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(1) Myrmecobius, × 50. Tooth germ of functional canine, to the left of which is seen a slightly calcified rudiment of a tooth of an earlier generation. (After Leche, according to whose interpretation they represent germs of a milk canine and of a premilk canine.)

However, even granting this, there is a shadow of a doubt, for Marett Tims thinks that, inasmuch as in didelphys Röse has seen what he regards as three sets of germs, and it was the middle one which developed, it is possible that after all the milk teeth are suppressed, the permanent teeth developed, and a post-permanent set of vestigial germs developed in a greater degree and with more constancy than in other mammals.

This view does not, however, commend itself to me, as we have no analogy elsewhere for such a general suppression of the milk germs, with such a development of post-permanent vestiges. Still, the matter is open to argument.

Then came Leche's discovery that actual calcification, though of an abortive kind, does take place in Myrmecobius in germs which must be referred to an earlier series than the functional teeth.

As Leche held strongly to the view that the functional teeth of all marsupials are persistent milk teeth, he was hence compelled to interpret these rudiments as belonging to a "premilk" series, for they lay to the labial side of the functional germ; but this interpretation rests entirely upon the correctness of the identification of the functional teeth of the whole marsupial group as persistent milk teeth. But if the functional teeth of marsupials (which develop but one functional set) are permanent teeth, then Leche's premilk teeth become ordinary aborted milk teeth, and Myrmecobius merely stands alone among marsupials in having some calcification occurring in both sets.

Woodward thus puts the present state of ideas upon the subject of the premilk dentitions:—"In the anterior part of the jaw of the marsupials we find the following sets of teeth: (1) a small vestigial set, often calcified; (2) a large functional set; and (3) a series of lingually-placed swellings of the dental lamina (Kükenthal, Röse, Leche, and Woodward) closely resembling in appearance the first indication of the successional germs in the Placentalia. It is now generally believed that the second set represents the milk dentition and the third the reappearing permanent teeth of higher mammals, the first set being regarded as a premilk dentition. If the structures described by Röse and Leche in man, the ox, and the hedgehog, are the homologues of the calcified labial set of the marsupials, then there can be no doubt that this latter is a premilk dentition: but these structures in the Placentalia are slight, though said to be constant, and some may doubt the correctness of this interpretation, especially on comparing these labial teeth with the undoubted reduced milk dentition in many insectivores, and they may consequently be inclined to regard, as Tims has, the labial toothlets of the marsupials as reduced milk teeth, and thus revert to the discarded Flower and Thomas hypothesis. It will no doubt be difficult to convince such believers that their interpretation is incorrect until we can find some premilk teeth in the placentalia better developed than those of Leche and Röse, and we can only admit that ontogeny is not as yet conclusive on the point as one could wish."

And, finally, Messrs. Wilson and Hill, finding in Peramcles some vestiges (calcified) corresponding to those of Leche in Myrmecobius, and wholly denying the right of Kükenthal and Röse swellings to the lingual side of the functional germs to be regarded as tooth germs at all, reopen the whole question, and would say of the marsupials that they all present a more or less completely aborted milk dentition, and a functional permanent dentition homologous with that of placental mammals.

The following may be taken as a rough summary of present views on the subject:—

According to Leche's latest dicta, in marsupials the functional teeth belong to the milk dentition. There are rudiments, sometimes calcified, of a premilk set; of the "permanent" teeth one only is fully calcified, and often functional, the others are rudiments.

In Placental mammals there are but small traces, never calcified, of a premilk series. The milk teeth (with the possible exception of the true molars (see p. 367)) never persist through the whole life of the animal, but a "permanent" set replaces them in the adult animal. A "post-permanent" set is represented in some by bands beyond the permanent tooth germs, but these never calcify. The milk dentitions occur in various degrees of reduction, thus:

a. One (for instance, dpm_1 in most mammals) or more (*e.g.*, Erinaceidæ) fail to attain to full calcification, without the rest of the milk teeth being aborted.

b. The whole milk dentition (except, as above, the true molars) is more or less rudimentary, as in Pinnipedia; and in some forms is absorbed without even being cut, as in some Phocidæ, Rodents, and Chiroptera.

c. The milk dentition is neither represented by rudimentary nor by erupting teeth (? Bradypus).

d. The milk dentition (except the true molars) does not attain to any calcification at all (Shrews, many Rodents).

This is a considerable modification of Leche's earlier views, but it does not meet with universal acceptance. Thus Kükenthal (and Leche formerly) holds that the teeth of Cetacea are milk teeth, and that it is the permanent series in them which is suppressed; though Leche regards it as still somewhat an open question. And Wilson and Hill hold that it is the milk series which is suppressed in marsupials, and that their functional teeth are the "permanent" series; moreover they dissent from the view that the true molars are homologous with the milk series.

As regards the true molars, several ideas have been propounded.

1. That, as suggested by Owen and others, these teeth having had no predecessors, and having (Kükenthal, Röse, Leche, &c.) arisen from the primitive tooth band must be regarded as members of the milk series.

2. That they belong to the second in replacing dentitions (Woodward, Magitot, &c.).

3. That they are not homologous with either, but represent the two series by a fusion of germs, *i.e.*, by a using up the material whence two series might have been formed (Kükenthal (late view), Schwalbe).

4. That each true molar is the terminal member of a separate series of successive ages.

This, again, must be regarded as still a question *sub judice*, but I am myself inclined to regard them as members of the permanent series, not attaching great weight to the presence of undifferentiated lingual swellings of the tooth band beyond them, and regarding it as more likely that the more persistent permanent series should have remained than that milk teeth should have done so.

There is a reason, or some show of a reason, for the succession taking place as far back as the premolars, and the molars being exempt from change, which, so far as I know, has not been noticed by any of the many writers upon the subject. In all mammals the whole length of the jaw, at the time of birth and afterwards, is occupied by tooth germs and afterwards by teeth; it is well ascertained that the manner of growth in the jaw is by backward elongation, and that that portion which is occupied by the molars actually does not exist at the time of birth, so that the tooth band, boring backwards in this region, dips down and has to lose its vertical connection with the epithelium of the surface. Tooth change might therefore be expected to be limited, as in fact it is, to that portion of the jaws which exists early, while the animal is small; a succession of teeth could not exist in the molar region, because during the reign of the milk teeth in front the molar region itself does not exist.

If we consider that the point of the primitive Diphyodontism of the mammals is established, and that they are probably descended from polyphyodont ancestors, no further explanation of the existence of successional teeth is called for. But the view propounded by Baume and adopted by Oscar Schmidt should just be noticed. They suggest that the two dentitions were originally disposed in line, and that the origin of successional teeth can be traced back to the shortening of the facial region, which gave no room for the full number of tooth germs to lie side by side: the result of this crowding being that they came to lie upon the top of one another, each alternate one becoming displaced and retarded; then that the teeth lying nearest to the surface having to be used first get developed first, and thus the milk teeth are placed at a disadvantage owing to the hostile position of their successors, who cause their absorption and ejection.

The investigation of these questions is further complicated by the fact that there are quite numerous instances of "permanent" teeth, that is teeth unquestionably belonging to the second set, which are shed off early, and do not remain in place through the lifetime of the animal; an example of this is to be found in the Wart Hog (Phacochœrus), which loses successively all its premolars and the first and second true molars, the last true molar alone being truly persistent.

It has already been mentioned that amongst homodonts no succession of teeth has been observed in the Cetacea; but Kükenthal states that the teeth of toothed whales

(Beluga, Tarsiops, and Globiocephus) are the milk teeth, inasmuch as germs of successional teeth which never cut the gum are to be found to their inner sides, while Leche considers the evidence of this insufficient.

In the Shrews the milk series is very greatly reduced (p. 490), while in the Bats the milk teeth are homodont and their successors heterodont. In the Edentates in which a succession is known, the first teeth are heterodont, their successors homodont. No succession is known to take place in any of the Edentata, save the armadillo, and in the very aberrant form, Orycteropus (see p. 374). Amongst heterodonts there are several Rodents which have no deciduous teeth, *e.g.*, the rat; the dugong has probably deciduous incisors, but no other milk teeth; the elephant has no vertical succession, save in the incisors, but instead has a succession of teeth from behind forwards in the molar region.

As regards the "premilk" and "post-permanent" germs, it may be repeated that both alike stand or fall according to the import attached to the prolongations of the dental lamina beyond the permanent tooth germs. If these swellings are not tooth germs, then there is nothing to lead us to speak of a post-permanent dentition, as no one has seen a well-differentiated tooth germ, much less any calcification in this region. Again, if they be not tooth germs, then the functional teeth of marsupials are ordinary permanent teeth, and the "premilk" germs of Leche, Woodward and others, described also, but not so styled by Wilson and Hill, which do go on sometimes to abortive calcifications, are merely the ordinary milk set in a certain stage of suppression. For my own part I regard both "premilk" and "post-permanent" rudiments as at present quite hypothetical, and the evidence insufficient to establish their existence. But the literature upon this subject has become so profuse, and the data require such detailed descriptions, that it is quite impossible to enter into the discussion in the pages of a small text book, so the reader must be referred to the original sources, of which he will find an excellent summary in Messrs. Wilson and Hill's paper.

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THE TEETH OF EDENTATA, CETACEA, AND SIRENIA.

THE TEETH OF EDENTATA (BRUTA).

Sloths, Armadillos, Ant-eaters.

The term Edentata was applied to the animals of this order to indicate the absence of incisors (teeth in the intermaxillary bone): though this is true of most of them, a few have some upper incisors, the suture between the maxilla and the premaxilla passing, in some Armadillos, behind the first upper tooth; but the central incisors are in all cases wanting. It is also stated that in Dasypus sexcinctus there are some rudimentary teeth in the incisor region which never cut the gums.

Some of them are quite edentulous; this is the case in the Mutica, or South-American Ant-eaters (Myrmecophaga and Cyclothurus), in which the excessively elongated jaws cannot be separated to any considerable extent, the mouth being a small slit at the end of the elongated muzzle. Food is taken in by the protrusion of an excessively long, whip-like tongue, which is covered by the viscid secretion of the great submaxillary glands, and is wielded with much dexterity. The Manis, or Scaly Ant-eater, is also edentulous; and it is said by Max Weber that the reduction has gone so far that no dental rudiments could be detected. Röse, however, examining Max Weber's sections, came to a different conclusion, and is of opinion that the slight epithelial thickening which he finds in them is to be interpreted as the preliminary to the formation of a tooth band, and in the lower jaw he has found it to grow in to form a small rudimentary tooth band. It, however, goes no farther, and but for the inherent probability, on the ground that edentulous mammals are almost certainly degenerated forms which have lost their teeth, that some remnants of original tooth formation would linger behind, the appearances would not be very significant.

The Edentata belong to the homodont section of mammalia, but in some certain teeth are more largely developed than others, so that there are teeth which might be termed canines. And whilst they are mostly monophyodont, at least one Armadillo has a succession of teeth, and so has the aberrant Orycteropus or aard-vark. Leche states that he has found in Bradypus a calcified but aborted predecessor to one tooth in front of the mouth, and Röse states that in all (Dasypus novemcinctus, D. villosus, D. hybridus, and Orycteropus) which have been microscopically studied, indications at least of successional germs have been seen. The teeth are of simple form, and do not differ in any material degree in different parts of the mouth, except only by their size (to this the canine-like tooth of the two-toed sloth is an exception). They are all of persistent growth, and therefore no division of parts into crown, neck, and root is possible: they consist generally of dentine and cement, with sometimes the addition of vaso-dentine, into which latter tissue the central axis of the pulp is converted; while in some members of the order other peculiarities of structure exist: thus in the Orycteropus (Cape Ant-eater), dentine like that of Myliobates is found; and in the Megatherium hard dentine, a peculiar vaso-dentine, and vascular cementum co-exist.

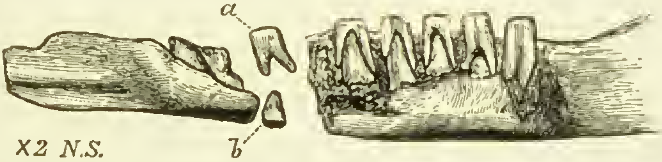
I am not aware that enamel has been seen upon the teeth of any Edentate animal, but I found some years ago that the tooth germs of the nine-banded armadillo were provided with enamel organs; this, however, proves nothing, for ("Philos. Trans.," 1876) I believe the presence of enamel organs to be universal and quite independent of any after formation of enamel. Röse, however, whilst confirming the absence of true enamel, holds that there is a mere glaze of structureless material (schmelzoberhautchen). And it is pointed out by Leche that in Tatusia the specialisation of the enamel organ goes on to the point of the internal epithelium becoming transformed into cylindrical ameloblasts, but that in Bradypus these cells remain roundish. It may be supposed, both from palæontological and developmental evidence, that the Edentata, so far as teeth are concerned, are a degenerated form; the shape of the tooth germs and of the unworn teeth suggests that they branched off from an early triconodont stage with numerous molars, diphyodont and heterodont, and furnished with enamel. They have suppressed the milk heterodont dentition, so that they are more or less completely monophyodont, and have established a homodont second series.

The teeth of the nine-banded **(T. peba) armadillo** will serve to illustrate the character of the dentition of the class. They are seven in number on each side of the jaw, of roundish form on section, and those of the upper and lower jaws alternate, so that by wear they come to terminate in wedge-shaped grinding surfaces: before they are at all worn they are bilobed, as may be seen in sections of the tooth germs.

In the accompanying figure the milk teeth are represented, and beneath them their permanent successors: the divaricated bases of the milk teeth are due to the absorption set up by the approach of their successors, and not to the formation of any definite roots. Successional teeth have been detected in this armadillo only (except also in T. Kappleri, which is, perhaps, a mere variety).

In the armadillos the teeth are always of simple form and about thirty-two in number, except in Priodon, which has as many as a hundred teeth, a number altogether exceptional among mammals. The axis of the tooth is occupied by a sort of secondary dentine in which the tubes run almost longitudinally and are gathered into bundles.

FIG. 170 (¹).



Sloths have fewer teeth than armadillos, and these softer in character, the axis of vaso-dentine (which is well pronounced and sharply marked off from the peripheral dentine) entering more largely into their composition, and forming as much as half the bulk of the tooth.

The two-toed Sloth has $\frac{5}{4}$ teeth in each jaw, and these are nearly cylindrical in section and of persistent growth, while in the region usually occupied by a canine there is a tooth much longer and larger than the rest.

Sir W. Flower and Pouchet and Chabry had failed to discover any succession of teeth in the sloths, and I have myself, through the kindness of the late Professor Garrod, examined microscopically the jaws of a fœtal Cholœpus, in which the teeth were but little calcified, and failed to detect any indication of a second set of tooth germs. The probability is, therefore, that they are truly Monophyodont, unless Leche, examining younger embryos, which he desires, but has not obtained, should find further traces of an antecedent dentition.

(¹) Lower jaw of a young Armadillo (Tatusia peba), showing the milk teeth (*a*) in place, and their successors (*b*) beneath them. From a specimen in the Museum of the Royal College of Surgeons.

The true ant-eaters are all edentulous, but Röse has seen very faint indications of a possible tooth band in Myrmecophaga.

The **Orycteropus**, or Cape Ant-eater (Aard-vark), the peculiarities of whose teeth have already been alluded to, has about thirty-six teeth in all; but these are not all in place at one time, the smaller anterior teeth being shed before the back teeth are in place. Pouchet and Chabry found a rudimentary tooth in the incisor region.

They are cylindrical teeth of persistent growth and simple form, and, like the teeth of the Armadillo, interdigitate with one another.

The affinities of the Aard-vark are very uncertain; it is grouped with the Edentata, but it is a very aberrant form, not only differing strongly in the structure of its teeth, which resembles that of Myliobates, but in other zoological characters as well. Oldfield Thomas has discovered that it also displays a succession in its teeth. ("Proc. Royal Soc.," 1890.)

The milk teeth are rudimentary and probably quite functionless, but they become calcified, though it is doubtful if they ever cut the gum. Unlike the permanent teeth, they are not of the persistent growth type, but one at least, the most posterior, has two distinct roots. There are none in the premaxilla, but seven have been found in the maxilla, and four in the mandible on each side.

In structure they present an approximation to that of the functional teeth, and the last is molariform, the others being simple cones. So that Orycteropus is diphyodont and heterodont.

In former ages many Edentates existed of much larger size, and the teeth of some of the gigantic extinct Edentates were a little more complex in form and structure; thus the teeth of the Glyptodon were divided by longitudinal grooves, which in section rendered it trilobed; and the teeth of the Megatherium were likewise marked by a longitudinal furrow, and presented greater complexity of structure.

In their persistent growth, uniformity of shape, and absence from the intermaxillary bone, they strictly conformed with the teeth of recent Edentata.

Amongst the Eocene fossils from the Puerco region, Cope has found forms which connect the Edentata with other mammals so far as their dentitions go.

Thus Hemiganus (Cope) had certainly one, if not two, upper incisors, with enamel on their anterior faces only, and with closed roots, and a very large canine, with enamel all over its crown, though thin upon the back. The lower canine had closed roots and enamel limited to the front (it may have been worn off the back).

Psittacotherium had two incisors above and one below ; the enamel was limited to the front on the upper incisor, which wore to a chisel edge, and the lower incisor had enamel all over, but very thin on the back. The canines also enamel on the front, and, like the incisor, had closed roots, though it went on growing long. Thus in Psittacotherium (Cope) the external lower incisors had disappeared, and a more or less rodent type of dentition had become established.

In Calamodon, the lower canines were very large, scalpriform, with thick enamel on front and none on back, and of persistent growth ; premolars and molars rather hyposodont, with elongated roots, but not of persistent growth, and possessed of enamel in bands, thick cementum taking its place where it is deficient.

In Stylinodon (Cope) the molars were cylindrical with long bands of enamel, and were of persistent growth. According to Wortman (" Am. Journ. Natural History," vol. ix.) these primitive Edentata (Ganodonta, a disputed term) in their earlier forms had teeth with closed and divided roots, and enamel more or less complete ; in later forms the teeth become hyposodont, without roots, of persistent growth, and with enamel limited to vertical bands, while incisors were present in both jaws.

THE TEETH OF CETACEA.

This order is divided into two groups, namely, the toothed whales or Odontoceti, and the whalebone whales or Mystacoceti ; these two groups are sharply defined from one another.

No Cetacean is known to develop more than one set of functional teeth, and these, when present in any considerable numbers, closely resemble one another in form.

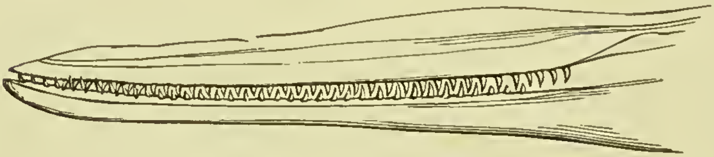
The teeth, however, of the extinct Zeuglodon and Squalodon, which have about 361 teeth, are heterodont in character.

Kükenthal has shown that at all events in Beluga, Tarsiops, and Globiocephalus, rudiments of successional teeth are to be found to the inner sides of the functional teeth, which latter are thus shown to be persistent milk teeth, though Leche considers it still an open question. It appears that they have descended from an ancient heterodont, diphyodont stock, and that they have suppressed the second dentition, establishing a homodont milk dentition which is persistent.

In Phocæna (common Porpoise) the enamel organs are not much differentiated, the internal epithelium remaining rounded, but in Balæroptera the differentiation goes further.

The teeth of Cetacea are usually composed of hard dentine, with an investment of cement; after the attainment of the full dimensions of the teeth what remains of the pulp is very commonly converted into secondary dentine; tips, and even entire investments of enamel, are met with in many of the order. The dentine is remarkable for the very numerous interglobular spaces which it contains; these are clustered in concentric rows, so as to give rise to the appearance of contour lines. The cement is often of great thickness, and the lacunæ in it are very abundant; its lamination is also very distinct.

Fig. 171 (1).



The **(Delphinus) Dolphin** may be taken as representing a generalised cetacean dentition. In it the teeth are very numerous, there being about 200: they are slender, conical, slightly curved inwards, and sharply pointed; as they interdigitate with one another there is very little wear upon the points, which consequently remain quite sharp. The largest teeth are those situated about the middle of the dental series.

Many variations in the number and form of the teeth are met with; the porpoise (Phocæna) has not more than half the number of teeth possessed by the dolphin. They are small, and have compressed crowns with cylindrical, contracted necks. The extent to which sockets, seldom very complete, are developed also varies greatly in the cetacea, in some there being little more than a continuous groove, in which the teeth are implanted. There is a little confusion in the nomenclature, the popular names, Porpoise, Dolphin, and Grampus being applied somewhat vaguely to several different genera. Thus the Grampus of sailors is the genus Orca of naturalists (the genus Grampus of naturalists is a quite distinct creature, with few teeth, and these only in the lower jaw, and is furnished with fewer teeth than the dolphin or the porpoise, but they are very large and stout, and exist in both jaws). The teeth of the **Grampus (Orca)** become worn down on their opposed surfaces, and coincidently with their wearing away the pulps become calcified. In the Oxford Museum there is a grampus in which, owing to a distortion of the lower jaw, the teeth, instead of interdigitating, became exactly opposed to one another ; the consequence of this was that the rate of wear was greatly increased, and the pulp cavities were opened before the obliteration of the pulp by calcification had taken place (2), so that the pulps died and abscesses around the teeth had resulted.

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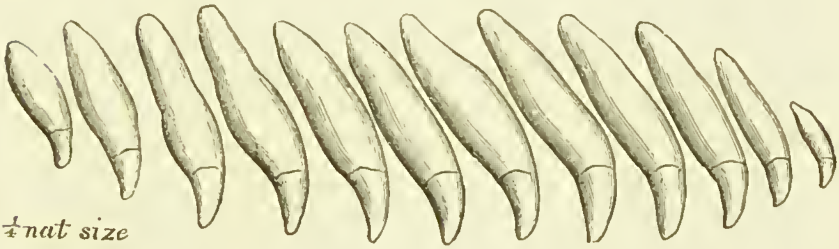
(1) Jaws of common dolphin (Delphinus).

FIG. 172 (1).



They are strong and fierce animals, attaining to a length of 20 feet, feeding on fish, seals, and other cetaceans smaller than themselves, and combining in numbers to attack even whales, which they thus succeed in killing.

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(1) Teeth of upper jaw of a grampus (Orca). (After Professor Flower.)

(2) "Trans. Odonto. Society," 1873. When I published this paper I was not aware that Eschricht had previously published a similar observation.

The remaining toothed cetaceans which will be noticed all present some reduction from the dentitions thus far alluded to.

The **sperm whale (Physeter)** grows to a gigantic size, 50 to 60 feet in length, and is pursued for the sake of its blubber, which yields sperm oil, and for the oil contained in the cells of its head (spermaceti); it feeds on large and even gigantic cuttle fish, and upon fish, which as a rule it swallows whole without biting them, as might be expected from its inefficient dental armament.

The teeth are numerous in the lower jaw, but in the upper jaw there are only a few curved, stunted teeth, which remain buried in the dense gum. The teeth of the lower jaw are retained in shallow and wide depressions of the bone by a dense ligamentous gum, which, when stripped away, carries the teeth with it. Thus every intermediate stage between this slight implantation and the well-developed stout sockets of the grampus, is met with in the Cetacea.

In the bottle-nosed whale (Hyperoodon bidens) the only large teeth present are two conical, enamel-tipped teeth (sometimes four), which remain more or less completely embedded within the gum, near to the front of the lower jaw; in addition to these there are 12 or 13 very small rudimentary teeth loose in the gums of both jaws. (Eschricht, Lacépède.)

The **Ziphoid cetaceans** present one of the most curious and inexplicable dentitions to be found in any animal. The upper jaws are edentulous, as in the Hyperoodon, and the lower jaws contain only a single tooth upon each side; but these teeth have attained to great proportions, measuring in full-grown specimens as much as ten inches in length; they are thin, flat, and strap-shaped, straight for some considerable part of their length, and then curving over towards each other; they even cross each other above the upper jaw so that they actually limit, and that to a very small amount, the extent to which the jaws can be opened.

It is not merely difficult to see what use these teeth can be, but it is hard to suppose that they can be otherwise than actually detrimental to their possessors in the pursuit of food ; but there is some reason to suppose that the presence of well-developed tusks is a character of the male sex, though upon this point the evidence is not quite complete. Females have been found with their skins curiously scored in two parallel lines, especially near the pudenda, suggesting the idea that they are liable to be attacked by the males.

The structure of these teeth is not less peculiar than their general form ; the summit of the tooth, which starts off nearly at right angles to the shaft (and so, the shaft being curved over the top of the upper jaw, comes to stand nearly vertically), consists of a denticle bluntly pointed, and made up of dentine coated with enamel. This denticle of triangular shape is only about a third of an inch in length, and in the adult specimen described by Professor Sir Wm. Turner had the enamel coat partially worn off.

In the *Challenger* Reports ("Zoology," vol. i.) he says, "In the earlier stage their structure does not differ materially from the ordinary type of tooth one meets with, say in the human or carnivorous jaw, the crown being formed by enamel, the fang by cement, whilst the great body of the tooth consists of dentine, in which is a marked pulp cavity, communicating with the exterior by a slit-like aperture at the root of the fang. The exceptional character these teeth exhibit in the erupted condition is due to the disappearance of the enamel from the crown, to the cessation in the development of the ordinary dentine, to the excessive formation of osteo-dentine, of modified vaso-dentine, and of cement, by means of which the pulp cavity becomes almost obliterated, and the fang assumes dimensions which, in the case of Mesoplodon Layardii, lead to the production of a tooth having the very remarkable form and relation to the beak which I have described."

As may be gathered from the above, the development of the tooth starts by the formation of the denticle, which is of an ordinary structure; the enamel, however, soon ceases to be formed, and, but very little further down, so does the true dentine; not, however, before cementum has begun to be formed upon its exterior. (See *c* in fig. on next page.) Then there comes an abrupt change in direction, and in the place of true dentine we find a coarser textured tissue which contains large vascular canals.

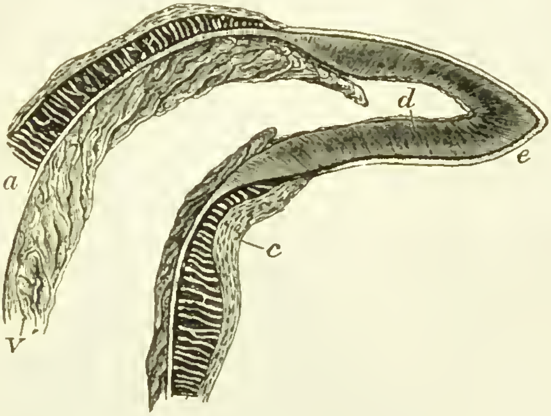
This Professor Sir W. Turner and Professor Lankester regard as a vaso-dentine, seeing that it is in all probability a product of the dentine pulp. Of this the great mass of the tooth consists, but it has throughout its length an investment of cementum of an ordinary type, which forms a complete exterior layer, laminated, full of lacunæ, and for the most part devoid of Haversian canals.

Immediately beneath this layer there is, if the distinction be not exaggerated in the drawing, a definite stratum of tissue of material thickness which is characterised by an abundance of vascular canals arranged perpendicularly to the surface (in Fig. 173 *a*), which is regarded by Professor Turner as belonging to the dentine group of tissue, *i.e.*, as being a vaso-dentine. But there is a difficulty in accepting this view, viz., that near to the denticle it is seen to lie distinctly outside the true fine-tubed dentine (see Fig. 173), which it overlaps to a considerable extent; now, if this tissue was formed by the dentine pulp we should have the anomaly of a pulp first forming a very vascular vaso-dentine, then changing to forming a fine-tubed normal dentine (which is exactly the reverse of what is met with in other creatures in which the pulp forms these two structures), and finally reverting to the building up of a vaso-dentine.

Judging by analogy this seems so improbable that in the absence of more positive knowledge and simply judging from the figure, I should be inclined to refer this layer to the cementum. Lower down in the shaft of the tooth anastomoses take place between the tubes of this layer and those of the unquestionable pulp products, but anastomoses between dentine tubes and enamel tubes, and between dentine tubes and cement lacunæ are of common occurrence in many animals, so that this communication does not prove anything as to their respective origin.

However, Professor Lankester lays stress upon the globular botryoidal structure of this layer, which he states shades off into the fine-tubed dentine, so that it may perhaps be regarded as an excessive development of the globular layer of dentine, rather than as a vaso-dentine. In reconciliation of the discrepancy between the two descriptions, it is suggested by Professor Turner that the vascular canals seen by him in this layer may have become obliterated in the presumably much older specimen described by Professor Lankester.

FIG. 173 (1).



The central pulp cavity becomes reduced to the merest traces, so that the completed tooth is almost solid.

In the **Narwal (Monodon monoceros)** two teeth alone persist, and these are in the upper jaw. In the female the dental germs become calcified, and attain to a length of about eight inches, but they remain enclosed within the substance of the bone, and their pulp cavities speedily fill up. In the male, one tusk (in some very rare instances both) continues to grow from a persistent pulp till it attains to a length of ten or twelve feet, and a diameter of three or four inches at its base. This tusk (the left) is quite straight, but is marked by spiral grooves, winding from right to left. It is curious that in one of the specimens, in which the two tusks had attained to equal and considerable length, the spirals on the two wound in the same direction; that is to say, as regards the sides of the head, the spirals were not symmetrical with one another.

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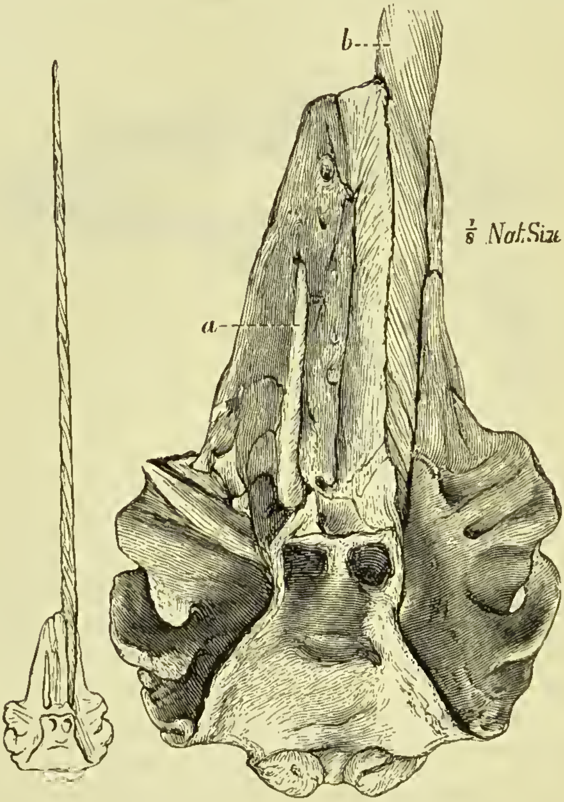
(1) Upper part of tooth of Mesoplodon. (After Professor Sir W. Turner.) *a.* Tissue of doubtful origin, permeated by vascular canals. *c.* Cementum. *d.* Dentine. *e.* Enamel. *v.* Vaso-dentine.

Fig. 174 (1).



The tusk of the male narwal may fairly be assumed to serve as a sexual weapon, but little is known of the habits of the animal.

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(1) Cranium of Narwal (Monodon monoceros). *a*. Stunted tooth, with its basal pulp cavity obliterated. *b* Long tusk. The small figure, giving the whole length of the tusk, shows the proportion which it bears to the rest of the skull.

Professor Sir Wm. Turner has lately noted the occurrence of two stunted incisor rudiments in a fœtal narwal: these obviously represent a second pair of incisors, and attain to a length of half an inch, but are irregular in form; they are situated a little behind the pair of teeth which attain to more considerable dimensions. All trace of this second pair of incisors is lost in adult skulls.

The remaining group of cetaceans, the Balænidæ or whalebone whales, are characterised by being, in the adult condition, destitute of teeth, but prior to birth the margins of both upper and lower jaws are covered with a series of nearly globular rudimentary teeth, which become calcified, but are speedily shed, or, rather, absorbed.

The fœtal teeth of the **Balænoptera rostrata (the Rorqual,** perhaps the commonest of the whalebone whales, which is sometimes stranded on British coasts, and has short and inferior whalebone) have been carefully described by M. Julin ("Archives de Biologie," 1880), the *Balænopteridæ* having been previously supposed to be without rudimentary teeth. The ramus contained forty-one tooth germs, each furnished with an enamel organ and dentine bulb, with a slight capsule; these were lodged in a continuous groove in the bone above the vessels, thus recalling the condition of the parts in a human embryo at a certain stage. A very small amount of calcification takes place, a mere film of dentine being formed upon the dentine bulb. But what is very remarkable is that the dentine bulbs are simple near the front, bifid in the middle, and trifid at the back of the mouth; in other words, these tooth germs would go to form heterodont teeth, not unlike those of some seals, or of Squalodon. Hence it has been suggested that the whale may be descended from some such ancestral form.

Kükenthal states that as these trifid teeth become absorbed they may separate into three. Moreover, he states that there are traces of successional rudiments.

From the upper jaw of an adult whalebone whale there hang down a series of plates of baleen, placed transversely to the axis of the mouth, but not exactly at right angles to it. The principal plates do not extend across the whole width of the palate, but its median portion is occupied by subsidiary smaller plates. The whalebone plates are frayed out at their edges and collectively form a concave roof to the mouth, against which the large tongue fits, so as to sweep from the fringes whatever they may have entangled. The whale in feeding takes in enormous mouthfuls of water containing small marine mollusca; this is strained through the baleen plates, which retain the Pteropods and other small creatures, while the water is expelled. Then the tongue sweeps the entangled food from the fringe of the baleen plates, and it is swallowed.

When the mouth is closed the baleen plates slope backwards towards the throat, but when it is opened by their elasticity they spring downwards to a vertical position, so as to still fill up the mouth, and as the mouth closes and expels the water, they act as strainers.,

Each plate consists of two dense, but rather brittle laminæ, which enclose between them a tissue composed of bodies analogous to coarse hairs. By the process of wear the brittle containing laminæ break away, leaving projecting from the edge the more elastic central tissue in the form of stiff hairs.

Each plate is developed from a vascular persistent pulp, which sends out an immense number of exceedingly long thread-like processes, which penetrate far into the hard substance of the plate. Each hair-like fibre has within its base a vascular filament or papillæ; in fact, each fibre is nothing more than an accumulation of epidermic cells, concentrically arranged around a vascular papilla, the latter being enormously elongated. The baleen plate is composed mainly of these fibres, which constitute the hairs of its frayed-out edge, but in addition to this there are layers of flat cells binding the whole together, and constituting the outer or lamellar portion. As has been pointed out by Professor Sir Wm. Turner ("Proc. Roy. Soc. Edinburgh," 1870), the whalebone matrix having been produced by the cornification of the epithelial coverings of its various groups of papillæ, is an epithelial or epiblastic structure, and morphologically corresponds not with the dentine, but with the enamel of a tooth.

The whole whalebone plate and the vascular ridges and papillæ which form it may be compared to the strong ridges upon the palates of certain Herbivora, an analogy which is strengthened by the study of the mouth of young whales prior to the cornification of the whalebone.

It must not be supposed that, because in the Dolphins, &c., there is a simple homodont dentition, they are in any way the parent form of other mammalia. On the contrary, the possession of some amount of hair on the skin, the nature of the rudimentary teeth, and many other characters, point to their being extreme, and in some particulars, degenerated modifications of other, and probably terrestrial mammals, and Kükenthal goes so far as to give the opinion that the two groups, the toothed whales and the whalebone whales, have had a distinct origin.

Thus, like the Edentata, the Cetacea have become homodont and practically monophyodont by a retrograde process, and the superficial resemblance of their simple conical teeth to those of a reptile is misleading.

THE TEETH OF SIRENIA.

More nearly connected with the Ungulata than with any other order, but still rather widely removed from them, stands the limited order of Sirenia, aquatic mammals formerly termed Herbivorous Cetacea, a term rather objectionable, as they are not very nearly allied to the true Cetacea.

The order is now represented by two genera only, the Dugongs (Halicore) and the Manatees (Manatus), but a third genus (Rhytina) has only become extinct within about a century. Their teeth, and other points in their organisation, indicate that they are more nearly allied to the Ungulata than to any other group, though their peculiarities are such as to elevate them to the rank of a distinct order.

They are of large size, and frequent shallow water, such as the mouths of great rivers, their food consisting of seaweed and aquatic plants. Their incisors and molars, when both are present, are widely separated, and the former vary from being quite rudimentary to forming formidable tusks.

The dentition of the **Dugong** is in several respects a very interesting one: the front part of the upper jaw, consisting in the main of the intermaxillary bones, bends abruptly downwards, forming an angle with the rest of the jaw. This deflected end of the jaw carries two tusks, of each of which the greater part is buried within the alveolus. The tusk has an investment of enamel over its front and sides, but on the posterior surface of cementum only, so that in the disposition of the three structures it recalls the characteristics of a Rodent incisor, like which it is worn away obliquely so as to keep a constantly sharp edge, and, like which, it grows from a persistent pulp.

In the female, the tusks (incisors) do not project from the gum, their pulp cavities are closed, and the investment of enamel is complete over the whole top of the tooth.

The sloping surface of the upper jaw is opposed by the region of the symphysis of the lower jaw, which is of unusual depth. In this deflected part of the lower jaw there are eight or ten (four or five on each side) shallow and rather irregularly-shaped sockets, in which curved distorted teeth may be found in a fresh specimen, but it must not be from too aged an animal, as they eventually become eaten away by a process of absorption.

These abortive teeth are excellent examples of rudimentary teeth, as not only are they stunted, and even ultimately removed by absorption, but they are actually covered in by a dense horny plate which clothes this part of the jaw, and so are absolutely functionless.

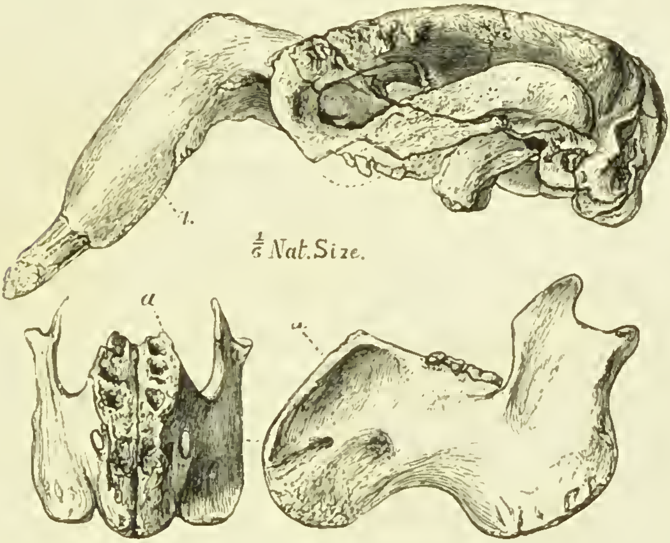
These horny plates, in their structure analogous to whalebone, are possessed also by the Manatee and Rhytina; on the free surface they are beset with stiff bristles, and are throughout built up of hair-like bodies welded together by epithelium.

Behind the region covered in by the horny plates, the

Dugong has five molar teeth on each side, of simple form, like those of the Edentata, and consisting of dentine and cementum only.

Their form is cylindrical, with the exception of the last, which is laterally grooved, but before they are worn they have tuberculated crowns, and they are of semi-persistent growth: thus they are evidently degenerating teeth, and in Rhytina they had wholly disappeared.

FIG. 175 (1).



By the time the last molar is ready to come into place, the first of the series is being removed by absorption of its root and of its socket. In aged specimens only two molars remain on each side of the jaws.

The Dugong is also peculiar as having a single deciduous tooth, namely, a predecessor to the incisive tusks; but it has been doubted whether it be not rather a rudimentary incisor than a milk tooth.

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(1) Side view of cranium and lower jaw of a Dugong (Halicore Indicus). From a specimen in the Museum of the Royal College of Surgeons. The surface of the deflected portion of the lower jaw, with its sockets for rudimentary teeth, shown both in front and in profile view, is indicated by the letter *a*; the corresponding surface of the upper jaw by the letter *b*.

The molar teeth of the Dugong consist of a central axis of vaso-dentine, a much larger mass of ordinary unvascular dentine, and a thick layer of cementum, but they do not share the peculiarities of the Manatee's tooth.

In the **Manatee,** just as in the Dugong, the front portion of the jaws is depressed and is covered in by a horny plate. The Manatee has i $\frac{2}{2}$, but they are rudimentary, and are buried under the horny plates which occupy the front of the mouth, and there are no canines. Gervais ("Hist. Nat. des Mammifères," vol. ii.) gives a larger number of rudimentary teeth, indeed as many as twelve.

And Kükenthal ("Anat. Anzeig," 1896) says that the rudiments which still exist show that the ancestors of the Manatee had three incisors—a canine and three premolars on each side in the lower jaw, but in the upper jaw reduction has gone yet further. He has found a milk dentition consisting of i $\frac{3}{3}$ c $\frac{0}{1}$ dpm $\frac{0}{3}$.

The molar teeth of the Manatee are much more numerous and more complex in form, and they approach to the configuration of the teeth of the Tapir very closely.

The Manatee has been said to have as many as forty-four molars, which are not, however, all in place at one time, the anterior ones being shed before the posterior are come into place; no vertical succession is known to take place amongst them.

It has long been known that teeth are shed off from the front of the series before the eruption of the hindmost tooth, so that though the creature develop at least forty-four molars there are seldom more than six in place at one time on each side.

But Mr. Oldfield Thomas ("Proc. Zool. Soc.," 1897) has lately described a yet more remarkable and, indeed, unique succession of teeth. By comparing the jaws of Manatees of various ages it is found that the successive teeth for a long time continue to increase in size, so that it is possible to more or less exactly identify the corresponding teeth in various specimens, although they have come to occupy different places in their order in the row, owing to the shedding off of teeth from the front of the series.

Compared in this way, the jaws of individuals of different ages give evidence of the development of at least twenty molar teeth on each side of each jaw, whilst in the very oldest available there was still always a tooth in reserve at the base of the coronoid process.

It seems impossible to resist the conclusion that the whole row of teeth is undergoing a perpetual migration forwards—the alveolar septa are very porous, whilst the outer shell of the jaw is very dense—and it would thus seem easy for the alveolar septa to be removed whilst the teeth move forward, guided by the unaltered bony walls on either side.

It has been mentioned that the teeth of the Manatee are tapiroid in external form; they also possess peculiarities in minute structure, which are unusual in mammalian teeth. In examining some teeth, I found that the dentine, to all intents and purposes of the hard unvascular variety, was permeated by a system of larger, or "vascular" canals, which were arranged with much regularity, and were most abundant near to the periphery of the dentine, where they communicated with one another. The dentinal tubes did not radiate from these vascular canals; they, so to speak, take no notice of them, so that there is an ordinary unvascular dentine with a system of channels, which are no longer pervious, having become obliterated and presenting the appearance of greatly elongated interglobular spaces. (See p. 76.)

The enamel of the Manatee is also somewhat remarkable for the absolute straightness of its enamel prisms in many parts of the tooth.

The Manatee has a curious manner of feeding; the halves of the upper lip, deeply cleft in the middle, are beset with short stiff bristles, and are used to tuck things into the mouth; when these fail the flappers are raised and used to assist.

The huge extinct **Rhytina**, a little more than a century ago abundant in Behring's Straits, was altogether without teeth, but was furnished with dense, strongly-ridged, horny plates.

The Sirenia were abundant in Miocene and Pliocene seas. Halitherium had molars somewhat like the Manatee, but had tusk-like incisors in the upper jaw. The front of the upper and lower jaws was deflected, as in Dugong and Manatee. The anterior premolars were small, simple, and cylindrical, and the molars more complex, and there was probably a vertical succession in the premolar region.

Psorastomus, a tertiary fossil form only known by the skull, was yet more generalised, and had a tapir-like dentition $i\,\frac{3}{3}\;c\,\frac{1}{1}\;pm\,\frac{4}{4}$ or $pm\,\frac{5}{5}\;m\,\frac{3}{3}$, and serves to link the Sirenia yet more closely with terrestrial mammals.

THE TEETH OF UNGULATA.

This is a group of animals of which a vast number of forms are extinct, and are only imperfectly known to us.

Recent discoveries, especially those of Professor Marsh, Cope, Osborn, Wortman and others, in the rich deposits of America have brought to light a very large number of strange and highly interesting forms, which, while they have not done away with the old division of Ungulates or hoofed mammals into the Artiodactyle (even-toed) and Perissodactyle (odd-toed) Ungulates, have brought within it, to a certain extent, Hyracoidea and Proboscidea, and have introduced a number of existing forms which will not fit into either of the old divisions.

Nowadays, provisionally, they may be grouped into Ungulata Vera and Subungulata.

The Ungulata Vera comprise—

(i.) Artiodactyles, or even-toed Ungulata	Hippopotamus, Pigs, Anoplotherium, Cows, Sheep, Deer, and other Ruminants.
(ii.) Perissodactyles, or Ungulata with an odd number of toes.	Horses, Tapirs, Rhinoceros, Palæotherium.

The distinction between the two groups is strongly marked, if living animals alone be considered; but, as Professor Huxley has pointed out, increasing knowledge of fossil forms has broken down the line of demarcation.

Then we have an ill-defined group of—

(iii.) Ungulata Polydactyla or Subungulata, comprising	Hyracoidea, Proboscidea, Amblypoda, Toxodontia, Tillodontia, &c.

The Amblypoda comprise a number of extinct animals of huge size, as big as elephants. Professor Cope includes in it Professor Marsh's order Dinocerata, and to it may perhaps be referred several forms whose affinities are very puzzling, such as Toxodon.

But fortunately it is not necessary in an elementary work on Odontology to do more than present the descriptions of the several creatures somewhere near their right places, and so the increasing difficulties of the classification of the Ungulata need not be discussed.

Of Eocene Ungulata it may be said that almost all possessed the full mammalian dentition, *i.e.*,

$$\text{i}\,\frac{3}{3}\;\text{c}\,\frac{1}{1}\;\text{pm}\,\frac{4}{4}\;\text{m}\,\frac{3}{3} = 44$$

and a few had more.

A great many of them have five toes, and were otherwise less specialised than modern forms.

Moreover, as we look at the patterns of the molar teeth, we find them far more simple, trituberculate or quadrituberculate crowns being the rule.

In the earlier forms the molars were short and distinctly rooted (bracyhdont). Those with much longer crowns, such as the horse, are termed hypsodont, and occur later. When the surfaces of the molars present blunt cones, they are termed Bunodont, and when they are lengthened out anteroposteriorly and curved, they are called Selenodont, *e.g.*, as in the sheep.

In the more generalised types, such as, amongst recent Ungulates, the pigs and the tapirs, the cheek teeth have the cusps low, so that in all stages of wear the bottom of the intervening valleys is in view; but in the long crowned teeth of ruminants, and the still longer ones of the horse the bottom of the valleys (in the latter case filled in with cementum) cannot be seen at all till the teeth are worn down.

In all existing Ungulates the quadritubereulate type of tooth has been reached, but amongst the earlier ones the trituberculate type still persisted, or at all events persisted in their immediate ancestry, if such forms as Phenacodus are regarded as the parent form of Ungulates.

The modern Ungulata are all fitted for a vegetable diet, though possibly a few forms may occasionally prey upon much weaker animals. Indeed, among the extinct Ungulata there are some which tend to bridge the gap between existing Ungulata and Carnivora, wide though it now is.

In Ungulates there is a tendency to the reduction of teeth in the front of the mouth, to the suppression of canines, and to a great development of cheek teeth, in relation to their vegetable diet.

In existing Ungulates the milk dentition is generally well developed, and in the case of modern domesticated animals remains in use for a long time.

THE TEETH OF ARTIODACTYLE UNGULATA.

Artiodactyle, or even-toed Ungulata, comprise, amongst living animals, pigs, hippopotami, camels, sheep, oxen, &c.

They are grouped into

- (i.) Bunodonts, or Suina, comprising Pigs and Hippopotami.
- (ii.) Selenodonts, comprising Anoplotheridæ and the Ruminants.
  - (a.) The Tylopoda or Camels.
  - (b.) The Tragulidæ (Chevrotains). Small deer of S. Asia, which are somewhat intermediate between the Suidæ and the deer.
  - (c.) Pecora, or sheep, oxen, and deer.

The primitive Artiodactyla all had forty-four teeth of brachydont type: in later geological times they became long-toothed (hypsodont) like recent sheep and oxen.

In Artiodactyle Ungulata the premolars differ markedly both in size and pattern from the true molars.

Of those Artiodactyle Ungulates which are not ruminants the common **Pig** may be taken as an example.

The dental formula is $i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}$, or perhaps $p\,\frac{4}{4}\;m\,\frac{3}{3}$.

The first premolar is a tooth about which there is a doubt whether it is a retained milk tooth or a permanent tooth which has not had a predecessor.

Of this tooth Lesbre ("C. Rend. d. Soc. d. Biologie," 1893) says that it is cut about the fifth month, after the milk molar, but before the replacing teeth. As there is no vertical succession in the case of this tooth, he regards it as a milk tooth which was delayed and dwarfed by the development of the great canine close to and below it. As a proof, he says that he has discovered in one case a successional tooth beneath it. The premolars of the Pig are cut in order from behind forwards, pm_4 being erupted first.

The dental formula of persistent or more or less persistent teeth would then read

$$\mathrm{i}\,\frac{3}{3}\;\mathrm{c}\,\frac{1}{1}\;\frac{\mathrm{dm}\,1}{\mathrm{dm}\,1}\;\mathrm{pm}\,\frac{3}{3}\;\mathrm{m}\,\frac{3}{3}.$$

Nawroth, as quoted by Marett Tims, says also that this tooth is occasionally replaced in the Pig, so that as a general rule we may say the young pig has dec. m. $\frac{4}{4}$, of which the first remains in place till the permanent dentition is nearly complete, and then falls out without having any successor.

The position of the upper incisors is peculiar, the two central upper incisors, separated at their bases, being inclined towards one another so that their apices are in contact; the third pair are widely separated from the inner two pairs of incisors. The lower incisors are straight, and are implanted in an almost horizontal position: in both upper and lower jaws the third or outermost incisors are much smaller than the others.

The lower incisors are peculiar in having upon their upper surfaces a strongly pronounced sharp longitudinal ridge of enamel, which gets obliterated by wear.

An interval separates the incisors from the canines, which latter are very much larger in the male than in the female, and in the wild boar than in the domesticated animal. Castration arrests the further development of the tusks; and the peculiarities as to size and direction which characterise the tusks of the adult animal are not represented in the canines of the milk dentition.

The form and direction of the canines are alike peculiar; the upper canine, which in its curvature describes more than a semicircle, leaves its socket in a nearly horizontal direction, with an inclination forwards and outwards. After rounding past the upper lip its terminal point is directed upwards and inwards. The enamel upon the lower surface of the tusk is deeply ribbed: it does not uniformly cover the tooth, but is disposed in three bands. The lower canines are more slender, of much greater length, and by wear become more sharply pointed than the upper ones: they pass in front of the latter, and the worn faces of the two correspond.

The lower canine is in section triangular, one edge being directed forwards, and its sides being nearly flat. Enamel is confined to the internal and external anterior surfaces; the posterior surface, which plays against the upper canine, is devoid of enamel, and the tooth is kept constantly pointed by the obliquity with which its posterior surface is worn away. The tusks of a boar are most formidable weapons, and are capable of disembowelling a dog at a single stroke, but they are greatly exceeded by those of the African Wart-hog (Phacochœrus), which attain to an immense size.

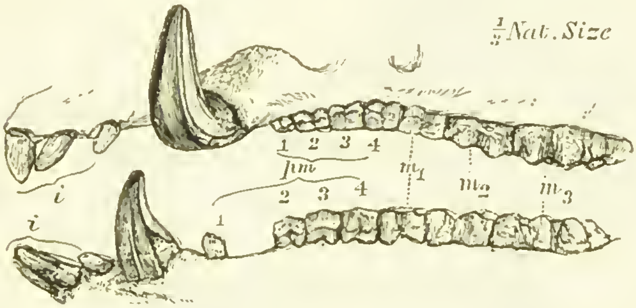
In the domestic races the tusks of the boars are much smaller than in the wild animal, and it is a curious fact that, in domestic races which have again become wild the tusks of the boars increase in size, at the same time that the bristles become more strongly pronounced. Mr. Darwin suggests that the renewed growth of the teeth may perhaps be accounted for on the principle of correlation of growth, external agencies acting upon the skin, and so indirectly influencing the teeth.

As in most Artiodactyles, the teeth of the molar series increase in size from before backwards: thus the first premolar (? milk molar) has a simple wedge-shaped crown, and two roots; the second and third by transitional characters lead to the fourth premolar, which has a broad crown with two principal cusps, and has four roots.

The first true molar has four cusps divided from one another by a crucial depression ; and the cingulum in front, and yet more markedly at the back, is elevated into a posterior transverse ridge. In the second molar the transverse ridge is more strongly developed, and the four cusps are themselves somewhat divided up into smaller accessory tubercles.

The last molar measures, from front to back, nearly twice as much as the second ; and this great increase in size is referable to a great development of the part corresponding to the posterior ridge or cingulum of the second molar, which has become transformed into a great many subsidiary tubercles.

FIG. 176 (1).



That such is a correct interpretation of its nature is indicated by our being able to trace the four principal cusps, though modified and not divided off, in the front part of the tooth, of which, however, they do not constitute more than a small part. Those Ungulates in which the surfaces of the molar teeth are covered by rounded or conical cusps, are termed "bunodonts," in contradistinction to those which present crescentic ridges on the masticating surface of their molars, and which go by the name of "selenodonts."

In the Wart-hog **(Phacochœrus)**, the genus with very large canines, the disproportion between the last true molar and the other teeth is yet more striking.

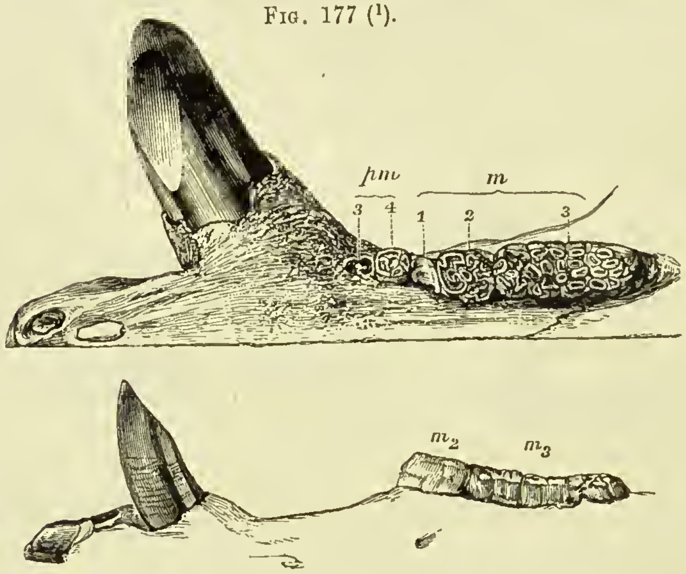
---

(1) Upper and lower teeth of wild boar (Sus scrofa). In this specimen the tusks are not so largely developed as they sometimes may be seen to be.

In antero-posterior extent the third molar equals the first and second true molars and the third and fourth premolars (the whole number of other teeth of the molar series possessed by the animal) together.

When a little worn its surface presents about thirty islands of dentine, surrounded by rings of enamel, the interspaces and the exterior of the whole being occupied by cementum.

Fig. 177 (1).



Of course, prior to the commencement of wear, each of these islands was an enamel-coated cusp.

The Wart-hog's dentition has, however, another instructive peculiarity ; the first true molar is in place early, and becomes much worn down (this is true, in a less degree, of the common pig, and indeed of most Ungulata). Eventually it is actually shed ; the same fate later befalls the third premolar and second true molar, so that the dentition in an aged specimen is reduced to the fourth premolar and the third true molar alone, and eventually to the last true molars alone. Thus, both in the great complexity of the back molars and the fact that the anterior teeth are worn out and then discarded, the Wart-hog affords a parallel to the anomalous dentition of the elephant.

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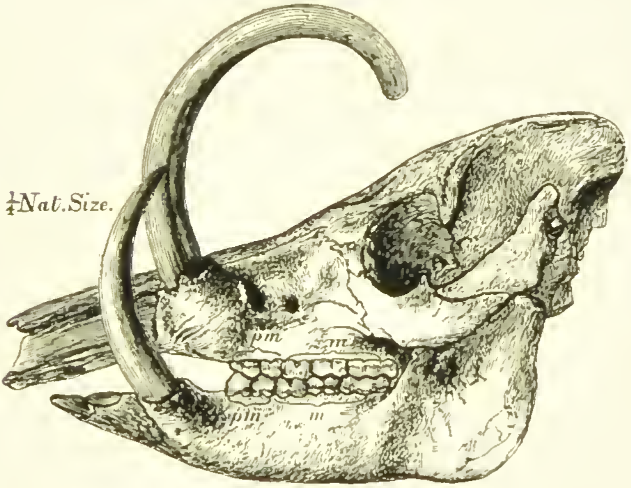
(1) Upper and lower teeth of Phacochœrus. In the upper jaw, the last two premolars, and the much-worn first true molar remain. In the lower all have been shed off, save the last two true molars. From a specimen in the Museum of the Royal College of Surgeons.

Phacochœrus presents the peculiarity that the tusks are large in both sexes.

As has already been noticed, the upper canines in the boar turn outwards and finally upwards, so as to pass outside the upper lip; this peculiarity in direction, yet more marked in Phacochœrus, attains its maximum in the **Sus babirussa.**

Fig. 178 (¹).



This creature, strictly confined to the Malay Archipelago, where it frequents woody places, has (in the male) the upper and lower canines developed to an enormous extent. The upper canines are turned upwards so abruptly that they pierce the upper lip, instead of passing outside it as in other Suidæ, preserve a nearly upright direction for some little distance, and then curve backwards, so that their points are directed almost towards the eyes.

The lower canines are less aberrant in direction and in shape, being somewhat triangular in section, but they also are

(¹) Skull of Sus babirussa (male). The upper incisors have been lost from the specimen figured; they are much like those of a pig.

of very great length, and pass upwards, far above the level of the snout; their points are also directed backwards, but have in addition an outward inclination. The canines are devoid of enamel, and grow from persistent pulps, a fact which sometimes has a disastrous result, for the tip of the tooth, occasionally taking a wrong direction, re-enters the head or the jaws of the animal.

The natives of Fiji make use of the persistent growth of the tusks of the Pig to procure as ornaments tusks which have grown into a ring: this is effected by extracting the opposing upper tooth.

Their length is very great; the animal is smaller than the domesticated pig, but its canines attain a length of eight or ten inches. Their use is a matter of conjecture; the position of the upper tusks has suggested the idea that they may serve as a protection to the creature's eyes, as it seeks its food, consisting of fallen fruits, among the brushwood. But were that the case the female also would probably have them, which is not the case, the upper canine being only about $\frac{3}{4}$ inch long, though it is everted and is beginning to turn upwards; the lower tooth is a little larger; and although in old animals they are often broken off, it is not certain that they are much employed in fighting. Its other teeth are in no respects remarkable.

Hippopotamus.—The dental characters, as well as others, indicate the affinity of the Hippopotamus to the Suidæ.

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3}.$$

The incisors are tusk-like, and bear but little resemblance to those of most other mammalia; they are nearly cylindrical, bluntly pointed at their apices by the direction of wear, and this is in some measure determined by the partial distribution of the enamel, which is laid on in longitudinal bands in the upper teeth, but merely forms a terminal cap on the lower incisors.

The upper, standing widely apart, are implanted nearly vertically: the lower incisors, of which the median pair are exceedingly large, are implanted horizontally.

The canines are enormous teeth; the lower, as in the Hog, are trihedral, and are kept pointed in the same manner; the upper canines are not so long, and the portion exposed above the gum is relatively short.

The incisors and canines are all alike teeth of persistent growth.

The premolars, of which the first is lost early (being, like the similar tooth in the pig, perhaps a milk molar), are smaller and simpler teeth built up on the same type as the true molars.

These latter, especially when worn, have a very characteristic double trefoil pattern; the four cusps, in the first instance, were separated by a deep longitudinal and a still deeper transverse groove; each cusp was, moreover, trilobed; the first result of wear is to bring out the appearance of four trefoils; next, when the longitudinal furrow is worn away, two four-lobed figures result; and finally all pattern becomes obliterated, and a plain field of dentine surrounded by enamel alone remains.

The teeth of the Hippopotamus are subject to a great amount of attrition, as is well shown by a specimen presented to the Museum of the Odontological Society, in which the molar teeth are all excessively worn. The Hippopotami use their incisors and canine tusks for the purpose of uprooting aquatic plants, of which their food mainly consists: the roots of these are of course mixed up with much sand, which wears down the teeth with great rapidity. The larger incisors and the canines are, and for centuries have been, articles of commerce, the ivory being of very dense substance and useful for the manufacture of small objects.

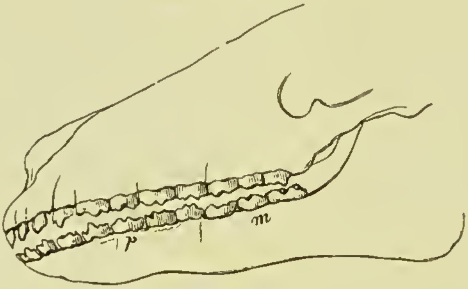
Anoplotherium is a genus of interest to the odontologist, because it possessed the full typical mammalian dentition, as far as the number of the teeth went; the teeth were of nearly uniform height, none strongly differentiated from those nearest to them; and they were set in close contiguity with one another, so that there was no "diastema."

The lower molar teeth of the Anoplotherium are built up on the same type as those of the Rhinoceros, and present the same double crescent; the upper molars are also referable to the same fundamental forms, though the difference is greater. The laminæ (transverse ridges) oblique in the Rhinoceros, are in Anoplotherium still more oblique, so that they become more nearly parallel with the outer wall, and an accessory pillar is developed at the inside of the anterior laminæ.

Not very widely removed from Anoplotherium is **Oreodon** (Cotylops), an Ungulate of Eocene age.

Like a good many tertiary Ungulates (both artiodactyle and perissodactyle) it had the full typical number of teeth, forty-four; but its interest to the odontologist is enhanced by the co-existence of strongly-marked canines with molars very much like those of ruminants, a group almost always devoid of canines.

FIG. 179 (¹).



In the upper jaw Oreodon had

$$i\,\frac{3}{\ }\ c\,\frac{1}{\ }\ pm\,\frac{4}{\ }\ m\,\frac{3}{\ }$$

i.e., the typical number of each kind of teeth. But in the lower jaw the first *four* teeth are like incisors, and the tooth which is like a canine is not the tooth corresponding to the upper canine, but to the small upper first premolar.

This is a fair illustration of the fact that although in nature it is generally the same tooth which is modified to perform the function of a canine, it is not invariably the

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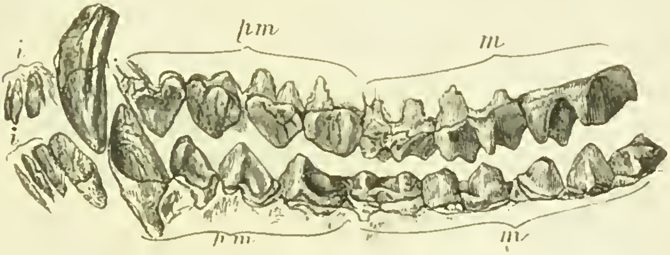
(¹) Side view of the dentition of Anoplotherium. (After Owen.)

same; for here in the same animal are two different teeth in the upper and lower jaws thus respectively modified.

And as they are different teeth, it happens that the upper (canine) closes in front of the lower.

There is reason to believe that there was some difference in the size of canines between the male and female Oreodon.

Fig. 180 (¹).



The remaining Artiodactyle Ungulates (Selenodont) are divided into the Tylopoda (Camels), the Tragulina and Pecora, though the transitional forms linking the Bunodont Ungulata with the Selenodonts are abundant in the Tertiary epoch.

The **Camels** have both upper incisors and canines, the dental formula being:—

$$i\,\frac{1}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{2}\;m\,\frac{3}{3}.$$

The first two pairs of upper incisors are absent, but the third or outermost pairs are present, and are rather caniniform in shape. In quite young skulls six upper incisors are present, but the two inner pairs are lost very early. The canines are strong pointed teeth, and the lower canine stands well apart from the three incisors of the lower jaw, unlike the fourth tooth in front of the mandible of typical pecora. (See Fig. 181.)

Of the three premolars which are found in the upper jaw the first (probably pm_1) is close behind the canine: it comes but once, is not acquired till about the sixth and seventh year, and persists through the life of the animal; and as

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(¹) Upper and lower teeth of Oreodon Culbertsonii. (After Leidy, "Smithsonian Contributions," 1852.)

there is said to be a trace of a follicle of a milk tooth preceding it, it belongs doubtless to the second series.

The second premolar is absent, the third being separated by a long interval from the first.

The third premolar is sometimes lost early, but the fourth persists.

The molars of the Camel are of the "Selenodont" type; a type the derivation of which from the several cusps of a bunodont type is sometimes pretty obvious, but in other cases is more obscure. Thus Scott points out that in the case of some premolars the inner crescent appears to be derived from a folding round of the edges of the outer cusp, which is clearly the protocone; whilst in others it appears to be derived from the occurrence of extra cusps.

Fig. 181 ([1]).

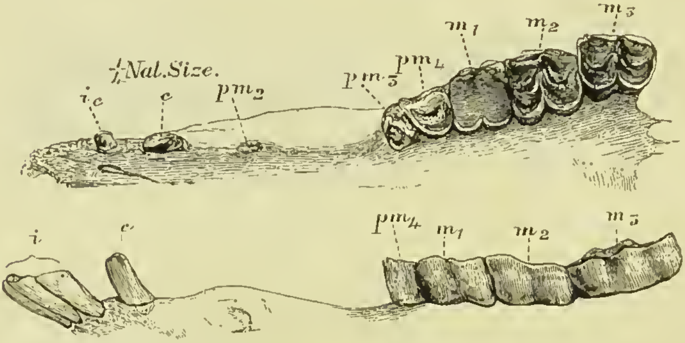
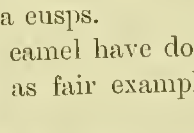


Fig. 182 ([2]).



The molars of the camel have double crescentic crowns, which may be taken as fair examples of simple ruminant

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([1]) Upper and lower teeth of a camel. In the figure pm^1 is lettered as pm^2, this being the former view of its homology.

([2]) Selenodont molar of a deer.

patterns, accessory pillars, &c., being added in some of the other families.

The Tragulina or Chevrotains, sometimes called Pigmy Musk Deer, though somewhat intermediate between the Pigs and Deer, and zoologically distinct enough, do not differ in their dentition from the true ruminants, with which they may be noticed here; the upper canines are well developed, especially in the males.

The hollow-horned ruminants (sheep and oxen and antelopes), and likewise almost all the solid horned ruminants (deer), have the following dental formula:—

$$i\,\frac{0}{3}\;c\,\frac{0}{1}\;\text{or}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The lower incisors are antagonised not by teeth, but by a dense gum which clothes the fore part of the upper jaw; if a sheep is watched as it feeds, it will be seen to grasp the blades of grass between the lower teeth and the gum, and then to tear them off by an abrupt movement of the head, as it would be impossible for it to, strictly speaking, bite them off.

The anomaly of the entire absence of upper incisors was held to have been diminished by the statement of Goodsir, who believed that uncalcified tooth germs were to be found in the fœtuses of many species. As this was precisely what might have been expected, it has since that time passed current as an established fact; but M. Pietkewickz, working in the laboratory of M. Ch. Robin, has absolutely denied the occurrence of even the earliest rudiments of tooth germs in this situation, after an examination of a series of fœtuses of the sheep and cow, ranging even from the earliest periods. ("Journal d'Anatomie," par Ch. Robin, 1873, p. 452.)

Miss F. Mayo ("Bull. Mus. Comp. Zool. Harvard," 1888) has re-examined this subject; she confirms the view generally accepted that the germs are absent, but she points out that in the region of the missing canine, differentiation proceeds a little further than in the incisor region, though it never attains to the formation of a real tooth germ, *i.e.*, that the suppression of the teeth has been progressive, and that the canine has been lost at a later period than the incisors. She bases this idea upon the occurrence of those knobs of epithelium which we are accustomed to find where an enamel germ is atrophying. Very numerous figures are given, so the reader may judge for himself of the material from which the conclusions are drawn.

Grouped with the six incisors of the lower jaw, and in no respect differing from them, rise the pair of teeth which are very arbitrarily termed "canines." As I cannot attempt to do more in these pages than give a bare outline of generally well-known facts, I have retained the usual dental formula,

$$i\,\frac{0}{3}\;c\,\frac{0}{1}.$$

Although the absence of upper canine teeth is a very general characteristic of ruminants, rudimentary canines exist in some deer, and I am indebted to the kindness of the late Sir Victor Brooke, a high authority upon the *Cervidæ*, for the following note:—

"The upper canines are present in both sexes in all the species of *Cervidæ*, with the exception of Alces, Rangifer, Dama, some smaller species of Rusa, Axis, Capreolus, Cariacus, Blastocerus, Coassus, and Pudu. The upper canines, when present, are, with the notable exception of Moschus, Elaphodus, Cervulus, and Hydropotes, small laterally compressed rudimentary teeth. Their crowns are in about the same stage of reduction as the crowns of horses' canines, but their roots are relatively much more reduced." Hence they are often lost in dried skulls, and it has generally been supposed that but few deer possessed canines at all.

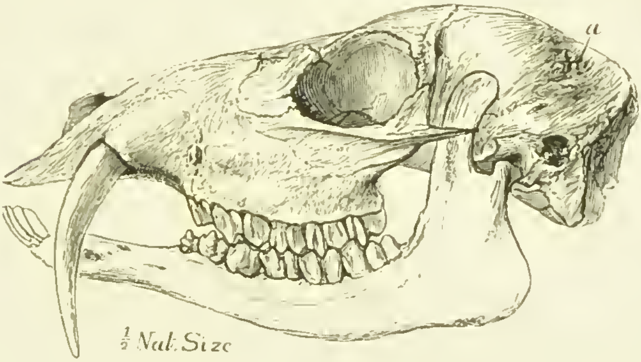
The hornless musk deer (Moschus) possesses upper canines of most formidable dimensions, while the female has very small subcylindrical canines.

The male pigmy musk deer (Tragulus) has large canines of persistent growth, the female small canines with closed roots.

The Indian Muntjac deer (Cervulus) has somewhat small horns, which are perched upon persistent bony pedicles, and it has upper canines which are curved outwards from beneath the upper lip, much as are the tusks of a boar; they do not, however, grow from persistent pulps, and are absent in the female.

Cuvier first pointed out that there was a relation between the presence of horns and the absence of canine teeth; the latter, serving as weapons of sexual combat solely, and being probably in no other way of service to the animal, are not required by an animal provided with powerful antlers or horns, whereas the absolutely hornless musk deer would be totally unprovided with weapons of offence were it not for his canines. To the musk deer and the Muntjac must be added Swinhoe's water deer, Hydropotes inermis, which has canines shorter and stouter than Moschus, and Michie's deer, Elaphodus cephalopus, another small hornless species, of which the males are furnished with formidable canine teeth, which are not so long as the Moschus, but are flattened from side to side, and are very strong.

FIG. 183 (1).



Although, with the foregoing exceptions, all the deer, oxen, sheep, antelopes, and the giraffe, animals constituting the greater number of the "Ruminantia," are without canine teeth, yet in the Camelidæ tusk-like canines are met with.

It is a character of the Artiodactyle Ungulata that the

(1) Cranium of male musk deer (Moschus moschiferus).

premolar teeth are of decidedly simpler form than the molars; in the ruminants the premolars may be said each to roughly correspond to one half of a true molar, and the premolars and molars form a continuous series.

In all true Ruminants the last true molar of the lower jaw has a third lobe (1), and the line of the outer surface of the row of teeth is rendered irregular by the anterior edge of each tooth projecting outwards slightly more than the posterior border of the one in front of it. And the deviations in the patterns of the surfaces of the molar teeth are so constant and characteristic that, although the common ruminant pattern is preserved in all, it is often possible to refer an individual tooth to its right genus.

The Ruminants all have a well-developed milk dentition, which serves the animal for a long time, indeed until after it has attained to its adult dimensions; thus a sheep has not completed the changing of its teeth till the fifth year, and a calf till the fourth year. But the first permanent molar is in them, as in so many other animals, the first of the permanent set to be cut, and comes up in its place at the sixth month (in the lamb), and hence has a long period of wear before any of the other second teeth are cut. Consequently the first permanent molar is, as seen in Fig. 181, invariably worn down to a much greater extent than the other permanent teeth; in the specimen figured it has been worn down below the inflections of enamel, so that it has lost its roughened grinding surface, and is reduced to a smooth area of dentine.

Not much is known of the structure of the dental tissues of the Ungulata which calls for mention in an elementary work. The thick cement of the crown of the teeth of the Horse, and indeed of most of the group which possesses thick cement, contains many "encapsuled lacunæ," and is perhaps developed from a distinct cement organ of cartilaginous consistence.

In the Cervidæ the true molars are somewhat brachydont, and these teeth take their place at once with the neck at the level of the margin of the gums, and remain at this level; the folds of the teeth are not much filled up with cementum.

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(1) Sir Victor Brooke informs me that Neotragus hemprichii, a small Abyssinian antelope, has only two lobes to the third lower molar.

In the Bovidæ teeth tend to be more hypsodont, and the tooth goes on growing up while a considerable part is worn away, so that the crown is lengthened and the root small; in this type of tooth the interstices of the columns are filled up with cementum.

The hypsodont tooth being in some respects a further elaboration of the brachydont, we find, as might be expected, that in the early and more generalised forms the teeth are shorter than in those which occur later, and every transition between the two may be found both in the Artiodactyle and Perissodactyle Ungulata. (Flower and Lydekker.)

Perissodactyle Ungulata.—These are much less numerous than the Artiodactyles, and amongst recent animals comprise only the Tapir, the Horse and the Rhinoceros and their allies.

In the Tertiary period, however, there were a much larger number, some of which bridge over existing gaps, and others of which became specialised along lines which have died out.

Their premolars and molars form an unbroken series; they are big, ridged or further complicated by various foldings, and the premolars, at all events the last three of them, are as complex in pattern as the true molars. The crown of the last molar is generally bilobed, and the tooth immediately behind the canine comes but once in the horse. In Rhinoceros it is sometimes replaced, but sometimes the milk tooth persists, while in the horse it is never replaced; nevertheless it appears to belong to the second series, as it is not cut until about the thirtieth month, that is to say, after the milk molars, and but shortly before the eruption of the second and third premolars.

The molar teeth are kept in an efficient state of roughness by the enamel dipping deeply into the crowns; by the cusps, in fact, being of very great depth. It consequently happens that after the immediate apex is worn away, the flattened working face of the tooth is mapped out into definite patterns, which, on account of the light thus thrown upon fossil remains often consisting of little else than the teeth, have been studied with great care. The result has been to establish a general community of type, so that, dissimilar as they at first sight appear, it is possible to derive all, or almost all, the configurations of their crowns from one or two comparatively simple patterns. But odontologists are not yet agreed, or rather are only getting to know enough of the vast number of extinct Ungulates which once existed (of which many have lately been discovered) to decide with certainty what the parent pattern was.

The patterns of the molars have been made use of to divide them into the following groups:

(i.) Bilophodont, *i.e.*, two ridges, *e.g.*, the Tapir.

(ii.) Molars (lower) bicrescentic, *e.g.*, Rhinoceros.

(iii.) Lower molar bicrescentic, with the addition of inner lobes or columns, *e.g.*, Horse.

The Tapir is interesting as appearing in Miocene strata and remaining practically unchanged till the present time, it being thus the oldest existing genus of mammals. (Flower.)

Tapir.—The dental formula is

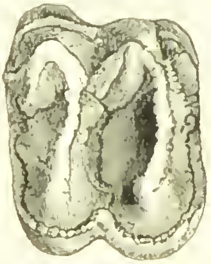
$$i\,\frac{3}{3}\,c\,\frac{1}{1}\,p\,\frac{4}{3}\,m\,\frac{3}{3}.$$

In a brief survey, like that to which the present work is necessarily confined, it will suffice to mention that there is no great peculiarity about the incisors or the canines, save that the third upper incisor is larger than the canine, and opposes the lower canine which ranges with the lower incisors; behind the canine comes an interval, after which come the premolars and molars, which are interesting, as being of simpler pattern than those of most Ungulates, and it will be necessary to very briefly allude to the various patterns characteristic of ungulate teeth, with a view of showing how they may have been derived the one from the other.

The first upper premolar is triangular, one of its cusps being suppressed, but the rest of them are squarish and resemble true molars. It has been preceded by a milk tooth, so that it is certainly of the second series.

In the Tapir four cusps are traceable, but ridges uniting the two anterior and the two posterior cusps are strongly developed, at the cost of the antero-posterior depression, *i.e.*, of one of the arms of the cross which separate the four cusps in other quadricuspid molars. There is therefore only a deep transverse fissure (hence it is called a bilophodont tooth), and the quadricuspid form is disguised. A low wall on the outside of the tooth connects the two ridges.

Fig. 184 (1).



According to the advocates of the tritubercular theory, the cusps present would be the protocone, paracone, metacone, and hypocone, united in pairs by transverse ridges.

In **Rhinoceros** the number of incisors varies, they being often almost rudimentary and not persistent, so that it is difficult to assign a dental formula to them :—

$$\mathrm{i}\,\frac{?}{?}\quad \mathrm{c}\,\frac{0}{1\,?}\quad \mathrm{pm}\,\frac{4}{4}\quad \mathrm{m}\,\frac{3}{3}.$$

In some fossil forms there are three lower incisors and a canine, so that it seems probable from comparison with them that the front lower tooth of the recent animal is the canine.

The first upper premolar is in some cases a replacing

(1) Molar tooth of tapir.

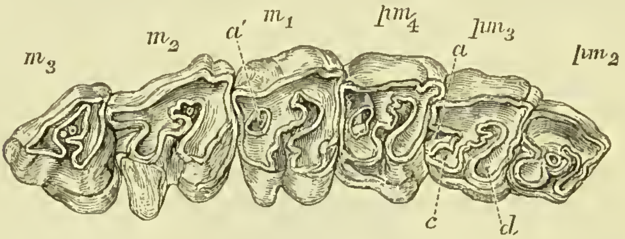
tooth; but in others, where the successional tooth is suppressed, the milk tooth persists.

In some of the earlier (Miocene) Rhinoceroses the first and second milk premolars are said to persist.

In the molars the external crest or ridge feebly present in the Tapir, becomes quite complete, the transverse ridges persisting but becoming oblique, hence the valley between the ridges *c* and *d* is also oblique, and a second valley comes in behind the posterior ridge.

The simplicity of the pattern is also departed from by the margins of the ridges, and therefore the boundaries of the depressions, being waved and irregular.

Fig. 185 (1).



The lower molars of the Rhinoceros are made up of two crescentic ridges, one in front of the other, with the hollows turned inwards. It is less obvious how this pattern is derived from that of the Tapir, but it may be that the transverse ridges of the Tapir type of tooth may have become curved and crescentic, so that the original outer edge of the posterior ridge abuts against the back and the exterior of the ridge in front of it. The valleys between the processes of enamel and dentine of the tooth of the Rhinoceros, termed "sinuses," are not filled up solidly with cementum.

The Palæotherium type of tooth may be said to be arrived at by the outer wall becoming zigzag, being bent inwards opposite to the cusps, and outwards at the corners of the tooth and opposite to the interspaces between the cusps.

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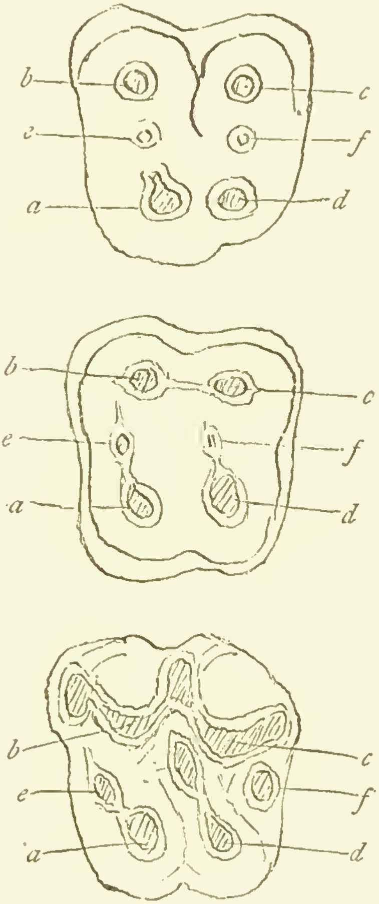
(1) Grinding surfaces of upper molar series of a rhinoceros. *a*. Posterior sinus, which at *a* has become an island by wear. *c*. Posterior ridge. *d*. Anterior ridge.

The more complex pattern which characterises the molar of the Horse may be derived from a further modification of the Rhinoceros molar.

To use the words of Professor Huxley: "Deepen the valley, increase the curvature of the (outer) wall and laminæ (transverse ridges), give the latter a more directly backward slope; cause them to develop accessory ridges and pillars; and the upper molar of the Tapir will pass

Fig. 186 (1).



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(1) Description of figure. (After Osborn.) Teeth of Euprotogonia, Hyracotherium, and Anchitherium. *a.* Protocone. *b.* Paracone. *c.* Metacone. *d.* Hypocone. *e.* Protoconule. *f.* Metaconule.

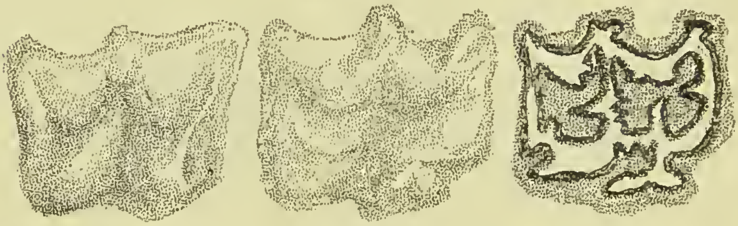
through the structure of that of the Rhinoceros to that of the Horse."

The preceding diagram, adapted from Osborn, will serve to show, in some measure, the stages by which such transformations of pattern are brought about.

In this, the simple tooth with its four principal cusps, and near to the middle of its crown the subsidiary cusps, is seen to be tending towards a lophodont type by the joining of these with the protocone and hypocone.

In Hyraeotherium this has gone further: the outer cusps are joined by a ridge (longitudinal), and the protocone and protoconule, and the hypocone and metaconule are joined by ridges (transverse, or rather oblique, to the line of the alveolus). At this stage the tooth is not far from that of the Tapir, or from that of Rhinoceros.

Fig. 187 [1].



In the third figure is seen the tooth of Anchitherium, one of the ancestors of the Horse. (See p. 414.)

In this all the ridges are more developed, so that the identity of the cusps is nearly lost; the external ridge has become sinuous and pillars have been added, conspicuously at its left hand end and less so at its right, while an additional detached pillar appears to the right.

By further increase in the obliquity and curvature of the ridges, and by the appearance of other detached pillars, the tooth pattern becomes transformed into that of Hipparion, in which two pillars on the inner side remain distinct, and

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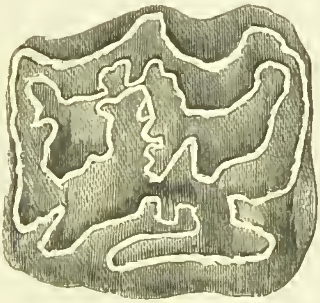
(1) Grinding surfaces of an unworn tooth of Anchitherium, of unworn tooth of horse, and of worn tooth of horse. In the latter the light areas are dentine, the shaded areas cementum, and the black border between them enamel. (After Flower and Lydekker.)

into that of the Horse, in which they become more or less fused with the curved ridges.

The outer ridge or wall is in the upper molar of the horse doubly bent, the concavities looking outwards. The transverse ridges start inwards from its anterior end and from its middle, and they curve backwards as they go to such an extent as to include crescentic spaces (between themselves and the outer wall). To this we must add a vertical pillar, which is slightly connected with the posterior end of each crescentic edge (these pillars are in Hipparion quite detached), and a second which is fused with the other crescent.

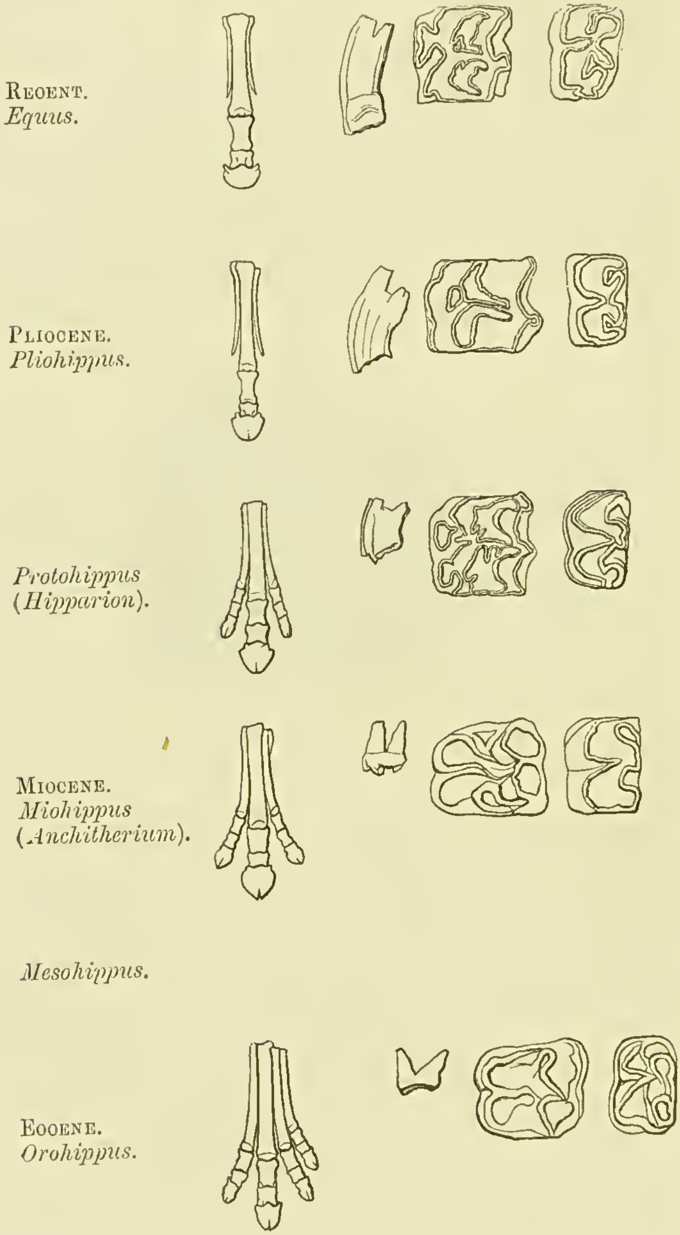
FIG. 188 (¹).



The lower molars of the horse present the double crescent, just like those of the rhinoceros, save that vertical pillars are attached to the posterior end of each crescent, thus slightly complicating the pattern of the worn surface. The interspaces of the ridges and pillar are in the horse solidly filled in with cementum. The extinct ancestors of the horse are now, however, pretty well known, thanks particularly to the researches of Professor Marsh; starting with the Eohippus, no larger than a fox, with four well-developed toes and a rudiment of the fifth (forefoot), through the Eocene Orohippus (four-toed), the Miocene Mesohippus as large as a sheep (three-toed, with rudimentary splint), the Upper Miocene Miohippus (three-toed), the Lower Pliocene Protohippus, as large as an ass (three-toed, but only the middle

(¹) Upper molar of horse.

Fig. 189 (1).



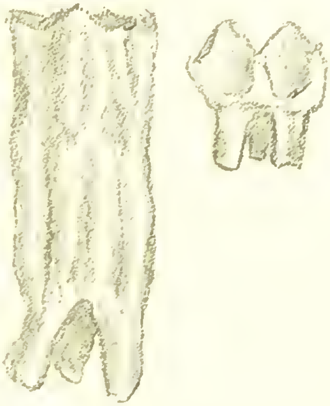
(1) Ancestry of the horse. (After Marsh.)
The forefoot and surfaces of upper and lower molars.

one reaching the ground), which was like the European Hipparion; then the Pliocene Pliohippus, which has lost the small hooflets, whilst in the Upper Pliocene the true Equus first appears.

Eohippus had forty-four teeth, the molars being quite distinct from the premolars, with short crowns and roots; (¹) in Orohippus the last premolar is like the true molars, while in Mesohippus two premolars are like the true molars.

Coincidently with the elaboration of the crown pattern a great lengthening of the crown (so that there was much more material available for wear) took place, but considerable crown elaboration had arisen before the teeth ceased to be brachydont.

Fig. 190 (²).



The great lengthening which has taken place in the hypsodont molars of the horse since the time of the Miocene Miohippus (Anchitherium) is well seen in the accompanying figure.

It is perfectly obvious that the hypsodont type of tooth provides for a much longer period of severe attrition before the roots are formed than the brachydont tooth of Miohippus, so that it is probable that the food of the modern horse is of a drier and harsher kind than that of its ancestors.

(¹) Ancient deer also had short crowns to their molar teeth.

(²) Outer view of second upper molar of Anchitherium (brachydont) and of horse (hypsodont).

In Miohippus the surface had two nearly transverse and slightly curved ridges with valleys between them, but the valleys were shallow and were not filled up with cementum.

As the crowns of the teeth became longer, and the valleys between the cusps very much deeper, they became filled up solidly with cementum, which not only added strength, but as the tooth wore down preserved a rough surface by affording three tissues of different hardness; for as the tips of the cusps wore down the enamel was worn off and areas of dentine surrounded by a rim of enamel became exposed, and the intervening cementum also came into wear, the efficiency of the surface for grinding purposes being yet further increased by the sinuosity of the enamel rings.

Equus.—The horse is furnished with the full mammalian number of teeth, the dental formula being—

$$i\,\frac{3}{3}\,c\,\frac{1}{1}\,p\,\frac{4}{4}\,m\,\frac{3}{3}.$$

The canines, however, are rudimentary in the female, whilst in the male they are well developed (in the gelding they are of the same size as in the entire horse); and the first premolar, which has no predecessor, is also rudimentary, and is lost early. A considerable interval exists between the incisors and the premolars and molars, which latter are very similar to one another, both in shape, size, and in the pattern of the grinding surface.

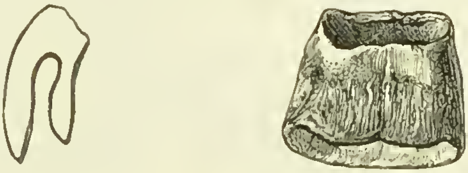
Mares occasionally have all four canines, but more commonly they have only the lower ones.

The incisors of the horse are large, strong teeth, set in close contact with one another; the teeth of the upper and lower jaws meet with an "edge to edge bite," an arrangement which, while it is eminently adapted for grazing, leads to great wearing down of the crowns. An incisor of a horse or other animal of the genus may be at once recognised by that peculiarity which is known as the "mark."

From the grinding surface of the crown there dips in a deep fold of enamel, forming a *cul de sac*. As this pit does not extend the whole depth of the crown, and the incisors of a horse are submitted to severe wear, the fold eventually gets worn away entirely, and the worn surface of the dentine termed the "table" presents no great peculiarity. But as this wearing down of the crown takes place at something like a regular rate, horse dealers are enabled to judge of a horse's age by the appearance of the mark upon the lower incisors. The "mark" exists in Hipparion, but not in the earlier progenitors of the horse. It is found in no other animal except a South American mammal of doubtful affinities—Macrauchenia.

A horse attains to its adult dentition very slowly. A foal is born with the two central incisors in each jaw; when nine weeks old it has four.

Fig. 191 (¹).



At 2½ years the temporary central incisors are shed, at 3½ the lateral, and at 4½ the corner incisors; and at 5 years the horse is said to have a "full mouth," the corner teeth having sharp edges. As the rate of wear is equal the mark gets worn out soonest upon the central incisors, and last upon the corner teeth.

At six the age is judged of chiefly by the wear of the corner teeth, as the cavity in centrals is nearly worn out. At the eighth year the central table is rather triangular, and the cups are gone from the middle incisors entirely, while from 8 to 10 years a stain remains on the centrals, and a round ring of enamel on the corner teeth.

After 12 years the mark has wholly gone, and there is no certainty as to age as far as it is concerned.

After the "mark" is worn away the centre of the tooth is marked by a difference of colour, due to the presence of

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(¹) Apex of crown of an upper incisor of a horse, not yet completely formed.

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secondary dentine, into which the remains of the pulp has been converted ; this lies in front of the site of the mark.

It is pointed out by Sydney Galvaine (" Horse Dentition ") that there is another reliable sign of age which comes into play after the wearing out of the cups of the lower teeth.

Upon the front surface of the upper incisors is a longitudinal median groove, which extends the whole length of the implanted portion, but stops short of the point of the crown.

Fig. 192 (1).

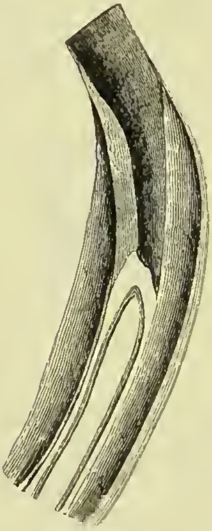
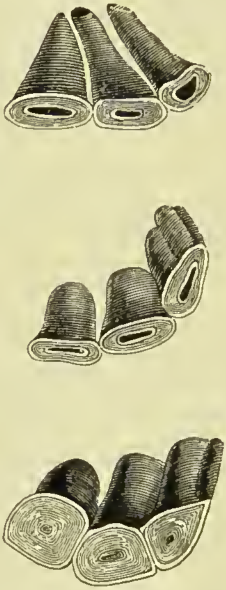


Fig. 193 (1).



Upon the centrals and middle teeth it is variable, but on the upper corner teeth it just appears at the margin of the gum in a ten-year-old. At this time there is about an inch of crown in view above it, and it takes eleven years to wear away this inch of tooth substance, so that at twenty-one years it reaches the working surface of the tooth. From what has just been said the reader will have inferred that the horse's incisors continue to be extruded from their sockets during the whole of its life, so as to meet the wear which is taking place.

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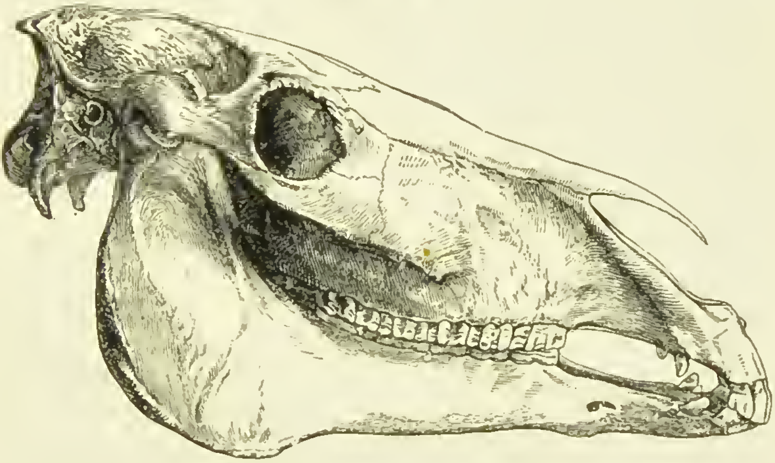
(1) Incisors of a horse, showing the marks at various stages of wear.

But they are not teeth of persistent growth in the ordinary sense, as the roots taper down to blunt points, and their full length is practically complete by the fifth year. It is, therefore, a process of gradual extrusion of an already fully formed tooth. It has been pointed out by my father that the enamel on the front of the tooth extends down to within a short distance from the end of the root: on the back of the tooth it stops short much sooner.

Fig. 194 (¹).



It is, however, overlaid by cementum, and is only brought into view upon the exposed crown of the tooth by the wearing away of this softer cementum, so that its existence has not been generally noticed. As the sides of the teeth are not exposed to wear, the cement covering remains upon them, nearly up to the working surface, while upon the back of the tooth again it is worn off, but only down to a point about three-quarters of an inch above its level on the front of the tooth.

While in the normal dentition the horse has only three premolars, yet a fourth, sometimes called wolf's tooth, is

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(¹) Side view of the dentition of a stallion. At a short interval behind the incisors are seen the canines; then, after a considerable interval, the premolar and molar series.

present at the front of the row, a remnant of the fuller dentition of Palæotherium and Hipparion.

When a bit is put into a horse's mouth it rests in the interval, or diastema, which exists between the incisors and the commencement of the molar series, and the great convenience of the existence of such a space has led many authors to assume that the horse was moulded in accordance with man's special requirements, so that it might be suited for its subserviency to his wants.

But the wide diastema appeared in the remote ancestors of the horse long ages before man's appearance on the earth, and the advocates of this theory of design would, as Professor Huxley suggests, have to tell us what manner of animal rode the Hipparion.

The molars of the horse are remarkable for their great length; they do not grow from persistent pulps, but nevertheless they do go on growing until a great length of crown of uniform diameter is made, subsequently to which the short and irregular roots are formed. As the upper working surface of the crown becomes worn, the tooth rises bodily in its socket, and when by an accident its antagonist has been lost, it rises far above the level of its neighbours. This elevation of the tooth takes place quite independently of growth from a persistent pulp, and, in fact, happens after the formation of its roots.

The pattern of the horse's molar has been already described. It should be added that the last molar differs from the rest in its posterior moiety being less developed than in the other teeth.

As each ridge and each pillar of the tooth consist of dentine bordered by enamel, and as the arrangement of the ridges and pillars is complex; as, moreover, cementum fills up the interspaces, it will be obvious that an efficient rough grinding surface will be preserved by the unequal wear of the several tissues.

If we had specimens of most of the Ungulates which ever lived, there would be no doubt as to the relationship of the various patterns: as it is, we are embarrassed by the lack of the material, which leaves gaps in some places too great to bridge over without some amount of speculation. As it is, Sir W. Flower divides the principal varieties ("Phil. Trans.," 1874) into three:—

(i.) That in which the outer wall is feebly developed, and transverse ridges become the prominent features, as in the tapir.

(ii.) That in which the outer wall is greatly developed and more or less smooth, the transverse ridges being oblique, as in the rhinoceros.

(iii.) That in which the outer surface and edge of the outer wall is zigzagged, or bicrescentic, as in the horse and palæotherium.

The milk teeth, as in all the Ungulata, are very complete, and are retained late; they resemble the permanent teeth in general character, but the canines of the horse, as might have been expected, their greater development in the male being a sexual character, are rudimentary in the milk dentition.

To the Perissodactyle Ungulates which are specially interesting on account of their dentition, must be added Homalodontotherium, a tertiary mammal of as yet uncertain affinities, the remains of which were described by Sir W. Flower. ("Phil. Trans.," 1874.)

It had highly generalised characters; its teeth were arranged without any diastema, and the transition in form from the front to the back of the mouth was exceedingly gradual, so that no tooth differed much from those on either side of it. Taking the pattern of its molar teeth alone into account, it would have been without hesitation declared to be very nearly allied to Rhinoceros, on which type they are formed, but the resemblance fails in the canine and incisor region, and it must be considered to be one of those generalised types related to Rhinoceros, to Hyracodon, and perhaps connecting them with such aberrant forms as Toxodon.

The largest of Ungulates more or less akin to the Perissodactyles equalled the elephant in size, and have been named by Professor Marsh Brontotheridæ or Titanotheridæ. The dental formula was

$$i\,\frac{2}{2}\,c\,\frac{1}{1}\,pm\,\frac{4}{3}\,m\,\frac{3}{3}.$$

The incisors were small and sometimes deciduous, and the canines short and stout, the lower being the more conspicuous owing to its being separated by a slight diastema from the premolars, which is not the case in the upper jaw.

The premolars in both jaws increased in size from before backwards, and did not differ from the molars next them. In the lower jaw the premolars and molars all consisted of two crescents, save the last, which had three crescentic cusps, and so were of the Palæotherium type. The molar teeth stood apart from those of any recent perissodactyles in their huge size, the squarish last upper molar, for example, measuring four inches antero-posteriorly and more than three transversely. (Professor Marsh, "American Journal of Science and Arts," 1876.)

THE TEETH OF HYRACOIDEA.

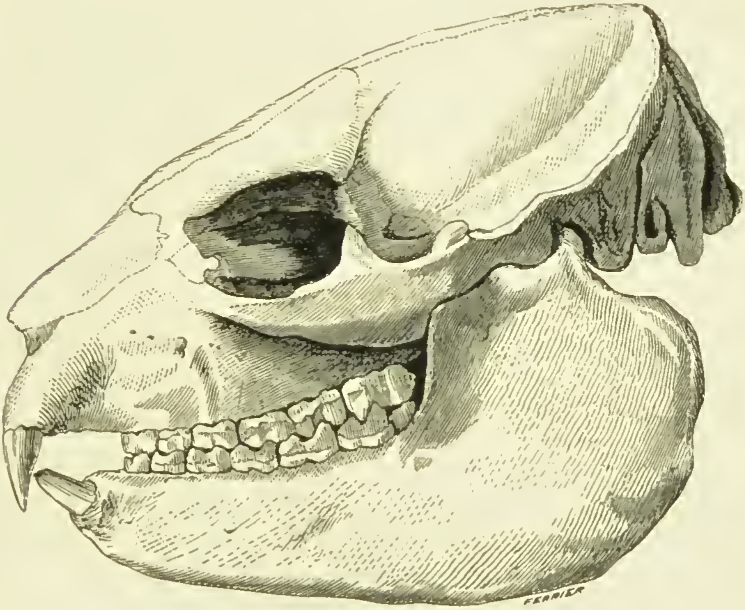
The Biblical coney (**Hyrax**), an animal as large as a rabbit, must not be passed over without mention, as its dentition has been indirectly the source of much controversy. So far as the pattern of its molar teeth goes, it corresponds closely with Rhinoceros, and was hence classed in close proximity to that genus by Cuvier. But a more extended survey of its characters has led to its being placed in a separate sub-order; it is a good example of the danger which attends relying upon any single character, such as the pattern of the teeth, as being alone a sufficient basis for classification.

All observers, however, are not agreed as to its position; it certainly presents affinities with Perissodactyla, but modern zoologists are pretty well agreed in placing it in a sub-order by itself. Professor Cope, however, regards it as closely akin to some early highly-generalised Ungulates, which he groups together by the name of Taxeopoda; they all possessed five toes on each foot, and many of the characters of their teeth bring them within measurable distance of ancient Insectivora.

The dental formula is $i\,\frac{2}{2}\;c\,\frac{0}{0}\;prm\,\frac{4}{4}\,m\,\frac{3}{3}$.

Seen from the side, the dentition bears some resemblance to that of a Rodent, because of the large size of its central incisors, which grow from persistent pulps, are chisel-edged, prismatic in section, and are furnished with a very thick coat of enamel on their antero-external and antero-internal faces: the second pair of incisors, which are small, are soon lost. But Hyrax has the full typical number of premolars and molars, and the patterns of these teeth are closely similar to those of the Rhinoceros.

Fig. 195 (¹).



In the lower jaw the middle incisors are small, and the outer ones largely developed, and all persist. Their crowns are in a manner trilobed, and they pass in ordinary closure of the mouth behind the upper incisors, where they are met by a dense pad of gum, but they are not of persistent growth.

(¹) Skull of the Hyrax.

CHAPTER XII.

THE TEETH OF PROBOSCIDEA.

At the present day the elephant stands alone, removed by many striking peculiarities from the Ungulata, to which it is more nearly allied than to other orders; but in former days the order Proboscidea was represented by a good many genera, was widely distributed over the globe, and transitional forms linking the elephant with somewhat less aberrant mammalia were not wanting. In this group the incisors grow from persistent pulps, and form conspicuous tusks; the elephant has i $\frac{1}{0}$, the Mastodon has i $\frac{1}{1}$, the Dinotherium i $\frac{0}{1}$.

Two striking features characterise the dentition of the Elephant; the enormous length of the incisor tusks, and the peculiar displacement from behind forwards of the molar teeth, by which it results that not more than one whole molar, or portions of two, are in place at any one time.

The upper tusks are preceded by small deciduous teeth; this is well established, though it has been recently denied by Sanderson ("Wild Beasts of India"). The milk incisors have their bases irregularly closed, and are shed off before the second year. When first cut they are tipped with enamel, but the enamel cap is soon worn off, and the remainder of the tusk consists of that modification of dentine known as "ivory," and of a thin external layer of cement. In some extinct species the enamel formed longitudinal bands upon the tusks.

The permanent tooth at the time of its eruption is coated with cementum, even over its enamel tip: this latter is about 5 mm. thick and extends for from 1 to 6 inches along the tusk.

In the Indian elephant the tusks are not so large as in the African species: and the tusks of the female are very much shorter than those of the male. In the African elephant no such difference in size has been established; and amongst Indian elephants males are sometimes met with which have tusks no larger than the females of corresponding size; they go by the name of "Mucknas." This peculiarity is not always transmitted, and it is known that in Ceylon tuskless sires sometimes beget "tuskers." Amongst the Ceylon elephants the possession of large tusks by the male is an exceptional thing, Sanderson stating that only one in three hundred has them, while amongst fifty-one Indian elephants only five were tuskless. The tusks are formidable weapons, and great dread of a "tusker" is shown by elephants less well armed.

A male makes use of his tusks for all sorts of purposes; thus, when a tamed one is given a rope to pull, he will, by way of getting a good purchase upon it, pass it over one tusk and grasp it between his molar teeth.

A pair of African tusks exhibited at the Great Exhibition of 1851, weighed 325 lbs., and measured 8 feet 6 inches in length, and 22 inches in circumference, but the average tusks imported from Africa do not exceed from 20 lbs. to 50 lbs. weight. Indian elephants seldom have tusks attaining very large dimensions; one was, however, shot by Sir Victor Brooke with a tusk 8 feet long, weighing 90 lbs.

The largest tusks were possessed by the Mammoth, the remains of which are so abundant in Siberia; these, which were strongly curved, and formed a considerable segment of a circle with an outward inclination, so as to well clear the sides of the head, attained the length of 13 feet, and a weight of 200 lbs. each.

Ivory is one of the most perfectly elastic substances known, and it is on this account that it is used for billiard balls; it owes its elasticity to the very small size of the dentinal tubes and the frequent bends (secondary curvatures) which they make; to this arrangement of the tubes the peculiar engine-turning pattern of ivory is due. The softer varieties of ivory contain 60·9 per cent. of lime salts, and the harder as much as 64·4 per cent. It is interesting to note that in the dentine of the molars, which have more need of roughness and less of elasticity, the percentage of lime salts is nearly as high as in human dentine. Ivory differs from other dentine in its containing from 40 to 45 per cent. of organic matter (human dentine contains only about 25), and in the abundant concentric rows of interglobular spaces. Along these ivory when it decomposes breaks up, so that a disintegrated segment of a tusk consists of detached concentric rings; in this condition many mammoth teeth are found, although sometimes where they have remained frozen and protected from the air until the time of their discovery they are hardly affected by the lapse of the thousands of years which have gone by since their possessors perished.

The last remains of the pulp are converted into dentine in which a few vascular canals persist; this of course occupies the centre of the tusk, and is small in amount.

The cementum which covers the tusks is rich in Sharpey's fibres.

The best ivory is that which comes from equatorial Africa; Indian ivory is not so highly esteemed, and Mammoth ivory is so uncertain in its degree of preservation that it does not find a ready sale, even though some samples almost attain the quality of recent ivory.

Even in Africa, though there is only one species of Elephant, the quality of the ivory varies: that from the West Coast being harder and more translucent, that from the East Coast softer, whiter, and more opaque.

The further from the Equator, the higher and drier the locality, the coarser the quality of the ivory: the best comes from the low and wet neighbourhood of the Gaboon.

The trade in ivory is quite an important one, the Board of Trade Returns for 1879 giving 9,414 cwts., of the value of £406,927, as the quantity brought to this country.

But the best of mammoth ivory, which has been preserved by the low temperature from any change, so that it is hardly distinguishable from recent ivory, has long been an article of commerce, perhaps even from the time of Pliny.

Nordenskiöld ("Voyage of the Vega") mentions that the dredge often brought up portions of tusks, and the natives offered at times very fine tusks for sale.

It is estimated that 100 pairs annually come thus into the market, and this is probably less than the real number. He travelled up the Yenisei in 1875 on board a steamer which carried over 100 tusks, of which, however, a large number were so blackened and damaged, that it was difficult to suppose them marketable.

The nearer you get to the Polar coasts the more abundant are the mammoth remains, especially where there have been great landslips, though the tusks found at the lowest latitudes are said to be smaller.

In the New Siberian Islands, in the space of a verst, he saw ten tusks sticking out of the ground, and from a single sandbank ivory collectors have for eighty years reaped a harvest.

In England dealers in ivory seem all to deny ever using mammoth ivory, though the finest specimens require the eye of an expert to distinguish them from recent ivory when cut up, and the denial must be taken *cum grano.*

One of the largest firms in Germany states that of imported mammoth ivory about 30 per cent. of the tusks are good and the remaining 70 per cent. worthless.

On breaking ivory across, the fractured surface presents parallel troughs and ridges, so that the amount of tissue broken through is much larger than it otherwise would be: this obviously adds to its strength, and is a result of the peculiar disposition of its much spirally twisted dentinal tubes: this may be well seen in specimens in which the tubes have been isolated. It is interesting to note in connection with the high percentage of organic matter in ivory that the connective tissue basis is very apparent, especially in secondary formations. (Miller.)

The surfaces of the tusks of the female are often deeply excavated about the level of the edge of the gum, and are sometimes so weakened from this cause that they break off. The late Professor Moseley told me that he was informed by the late Major Rossall, who as a sportsman had great knowledge of Indian elephants, that the tusks of all the females he has ever seen are so affected, and that the larvæ or pupæ of a dipterous insect are often found bedded in the gum, and attached to the surface of the tusk. There is a specimen of a female elephant's tusk with the pupæ attached in the Museum of the Royal College of Surgeons. It would be a matter of interest to ascertain whether the larva really eats away the tusk, or whether the wasting of the tusk be due to absorption set up by the irritated gum.

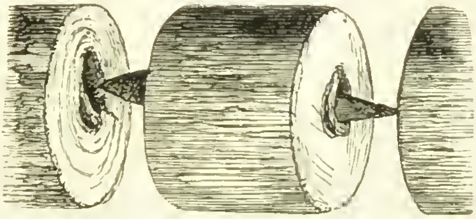
The tusks of an elephant are implanted in long and stout sockets, and grow from persistent pulps throughout the lifetime of the animal.

In the Indian elephant about one half of the length of the tusk is implanted, and in young animals the pulp cavity extends beyond the implanted portion, but in older animals it does not extend nearly so far. Thus, in one very big tusk the pulp cavity was a cup-shaped depression only 5½ inches deep, so that the tusk was virtually solid throughout. A knowledge of its extent is necessary, seeing that the tusks of captive elephants have to be shortened from time to time; this operation is by some done frequently, by others only at long intervals, such as ten years, in which case a large and valuable segment of ivory is cut off, and the end of the tusk bound with metal to prevent it from splitting.

Tusks sometimes exemplify on a large scale the results of injury to the growing pulp, as it is of no unfrequent occurrence that elephants which have been shot at and wounded escape.

The thin walls of the tusk near to its open end do not offer very much resistance to the entrance of a bullet; the result of such an injury is not, as might have been expected, the death of the pulp, but in some cases abscess cavities become formed in the neighbourhood of the injury, while in others less disturbance is set up, the bullet becomes enclosed in a thin shell of secondary dentine, or sometimes lies loose in an irregular cavity, and round this the normal "ivory" is deposited; upon the outside of the tusk no indication of anything unusual is to be seen, so that the bullets thus inclosed are found by ivory turners only when sawing up the tusk for use.

Fig. 196 (1).



As the tusk grows, that which was once in the pulp cavity, and within the alveolus, comes to be at a distance from the head, and in the midst of solid ivory.

As an example of the extent of injury from which a tooth pulp is capable of recovery, may be cited a specimen now deposited in the Museum of the Odontological Society, by Mr. Bennett, to whom I am indebted for permission to figure it.

It is to be presumed that a trap was set with a heavily loaded spear, or that it was dropped by a native from a tree, with the intention of its entering the brain of the elephant as it was going to water, both of these methods of killing elephants being practised in Africa. But in this case the spear penetrated the open base of the growing tusk, which looks almost vertically upwards (see Fig. 197), and then the iron point appears to have broken off. This did not destroy the pulp, but the tooth continued to grow, and the iron point, measuring no less than 7½ by 1½ inches, became so completely enclosed that there was nothing upon the exterior of the tusk to indicate its presence.

(1) Iron spear-head, irremovably fixed in the interior of a tusk, believed to be from an African elephant. From a specimen in the possession of Mr. Bennett.

I am told by Mr. Erxleben that he is acquainted with another instance in which a spear-head has become completely enveloped in ivory.

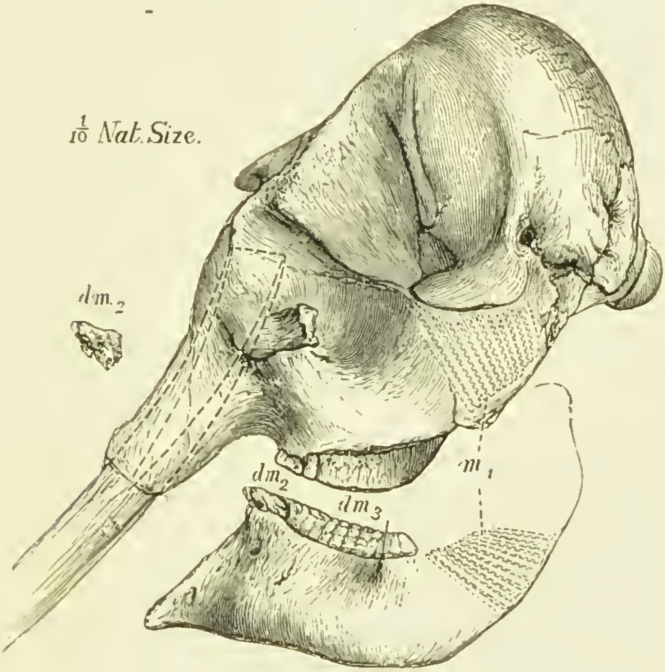
There are also other specimens extant, of which an excellent example is a javelin-head quite solidly embedded in the ivory, which is in the Museum of the Royal College of Surgeons.

Six molar teeth are developed on each side of the jaw by the elephant, and, arguing from analogy, they are sometimes classified thus—milk molars $\frac{3}{3}$, true molars $\frac{3}{3}$; occasionally a rudimentary tooth in front brings up the number to seven on each side. But the peculiarity of their mode of succession renders such a classification merely arbitrary, so far as the elephant itself is concerned, and it depends upon analogy with the teeth of the mastodon. Though the elephant has, during the course of its life, twenty-four molars, they are not all in place, nor indeed are they all actually in existence at the same time. Only one whole tooth on each side, or portions of two (when the front one of the two is nearly worn out), are in use at the same time. After a tooth has been in use for some time, and is worn away, a new tooth comes up to take its place from behind it, and absorption in the old tooth being set up, it is shed off, and the new tooth pushes forward into its place. (See Fig. 197.) Each successive tooth is of greater size than its predecessors: thus in the Indian elephant the first tooth has, on an average, four transverse plates; the second eight, the third twelve, the fourth twelve, the fifth sixteen, the sixth from twenty-four to twenty-seven. In the African elephant, in which the individual plates are much broader, they are fewer in number.

A reference to the accompanying figure will indicate how the succession takes place. The tooth in reserve occupies a position at an angle to that in use; as it moves forwards and (in the upper jaw) downwards its track forms almost the segment of a circle. Thus its anterior corner is the first to come into use, at a time when the position of the whole tooth is still exceedingly oblique, and the greater part of it is still within the socket.

The teeth as first formed consist of detached plates of dentine coated with enamel, the tops of which are mammillated ; these areas of dentine only coalesce after a considerable portion of their depth has been formed, and that portion of the tooth has been reached in which there is a common pulp cavity ; here dentine is continuous from end to end of the tooth.

FIG. 197 (1).



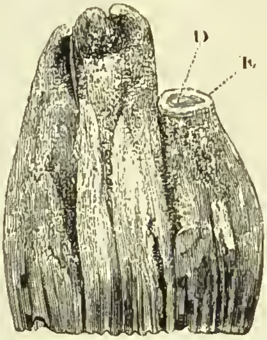
Just as the cusps of a human molar are separate when first calcified, so these exaggerated cusps or plates of an

(1) Side view of skull of young Indian elephant. The teeth in use are the second and third of the molars, which displace one another from behind forwards ; the anterior of these, corresponding to a milk molar in other animals, is nearly worn out ; the residual fragment is separately represented on the left. The tusk, of which only a short piece can be shown, is indicated within the socket by dotted lines, by which also the form of the pulp cavity is mapped out.

elephant's tooth are separate from one another till a great part of their length is completed, and they only coalesce when they reach the level of the common pulp chamber; in point of fact the elephant's tooth is mainly made up of its cusps, filled up solidly with cementum, the remaining portion being insignificant.

Several of these detached plates, such as the one figured below, are to be found at the back of the largest teeth even at a time when the front corner has been erupted and has come into wear.

Fig. 198 (1).



That the tooth is thus being built up only as it is required is of obvious advantage to the animal in diminishing the weight to be carried, and in economising space.

The teeth when they begin to be erupted do not at once come into use over their whole surface, but they come forward in an oblique position, so that the front corner of the tooth has been in use for some time, and its plates have been considerably worn down, before the back of the tooth has become exposed at all. Nay, more, in the case of the larger molars the front of the tooth is actually in use at a time when its back is not yet completed. And inasmuch as the tooth comes up not vertically but obliquely, and its anterior corner is first presented to wear, it follows that the whole of the tooth gets actually worn away, with the exception of a small fragment of its posterior buried corner, which is cast off.

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(1) Isolated plate (= exaggerated cusp) of an elephant's tooth, prior to its coalescence with neighbouring plates; at the top are seen its terminal mammillated processes, one of which has been cut off to show the central area of dentine, surrounded by enamel; at the base would be the open pulp cavity, not shown in the figure.

Had the tooth been erupted vertically, like other teeth, there would have been a comparatively large residue of implanted portion along its whole length to be cast off, so that its obliquity leads to a great economy of material.

Proboscideans formerly existed in which this peculiar succession from behind was to be found, at the same time that the ordinary vertical succession was not quite lost, and amongst these creatures (the mastodons) we are able to say with certainty which of the teeth are milk molars, which are premolars, and which are true molars. And mastodons pass by insensible gradations into the elephants, so that the line of demarcation between the two genera is an arbitrary one.

Mastodon.—In the later Tertiary periods this genus, approximating in its dental and other characters to the true elephant, was widely distributed over the world. The dental formula is not quite the same for all the genus, for in some (M. Americanus) no premolars existed.

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{2}{2}\;\text{milk molars}\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The upper incisors formed nearly straight tusks, seven or eight feet in length; the lower incisors also grew out horizontally from the front of the jaw, but in some species the lower tusks are rudimentary, are lost early, or are altogether absent, thus more nearly approaching to the condition met with in the elephant.

The several molar teeth of the Mastodon increased in size from before backwards. The crowns were built up of deep and strongly pronounced transverse ridges, of which the last molar had the largest number. The apices of the ridges, before being at all worn, were divided up into several blunt nipple-like (mastoid) processes, upon which the enamel was thick and dense, but the cement was thin, so that the interspaces of the processes were not filled up level by the latter tissue, as in the elephant.

Very definite roots were formed to the molars, the wearing down of the teeth being met by the worn teeth being shed off altogether from the front of the series, whilst new teeth were added to the back. Thus, just as in the elephant, the whole number of teeth were not in place at one time. Not more than three were in use at one time, and by the time the last and largest molar was cut, there was but one tooth remaining in front of it, and even this was soon lost, the dentition being thus reduced to a single molar on each side.

As the succession of the molars in the Mastodon affords a clue to the nature of the grinders of the elephant, it is necessary to add a few words about it. Some Mastodons had three milk molars, of which the last two were vertically displaced by premolars, just as in most other mammals, but the first milk molar was not so replaced (Mastodon angustidens). There appear to have been Mastodons in which no vertical succession at all took place, *i.e.*, in which there were no premolars, and others in which there was but one.

No doubt can be entertained as to the homologies of the teeth, even in those Mastodons which are not known to have any vertical succession, because analogy with those other species in which the second and third molars, counted from the front, were vertically displaced by nearly functionless premolars, tells us that the three front molars are milk molars. Now elephants develop six molar teeth on each side; the elephant is in the same case, quoad its molars, as the Mastodon Ohioticus, which had no vertical succession, so that we thus know the elephant's grinders to be—

$$\text{dm}\,\frac{3}{3}\;\text{m}\,\frac{3}{3}.$$

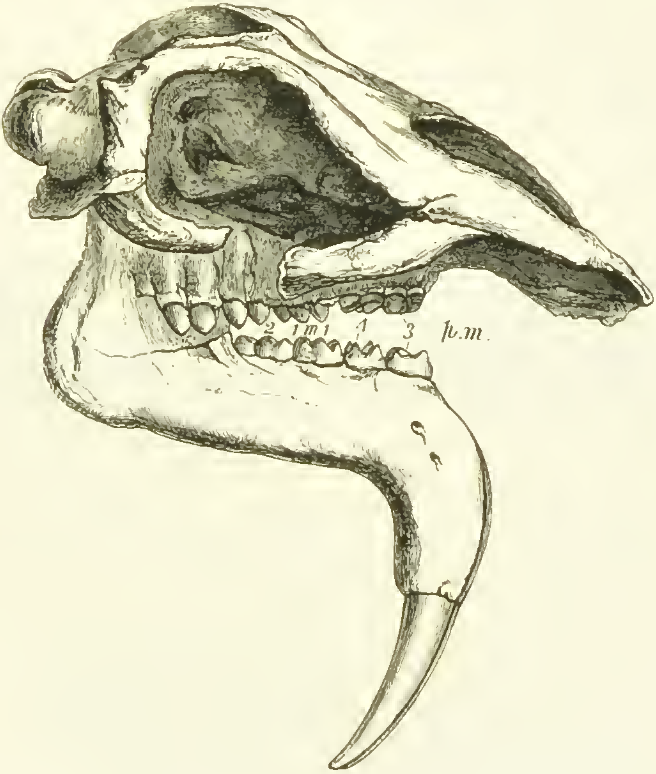
Dr. Falconer mentions an elephant from the Sewalik Hills (E. planifrons), in which two rudimentary premolars, of no functional importance, actually existed, and so the determination of the elephant's working teeth as

$$\text{dm}\,\frac{3}{3}\;\text{m}\,\frac{3}{3}$$

rests not only upon analogy, but upon actual observation.

The Dinotherium, a large animal, not unlike the Sirenia in the character of its cranium, and, like them, probably of aquatic habits, was remarkable for possessing large tusks, by analogy known to be incisors, in its lower jaw, none being present in the upper jaw. The tusks projected downwards at right angles with the body of the jaw, and were curved backwards. The portion of the jaw about the symphysis was deflected downwards, so as to afford an adequate implantation for these anomalous tusks.

Fig. 199 (¹).



The dentine of these tusks does not, however, present the characteristic ivory pattern.

The Dinotherium was as large as an elephant, and the

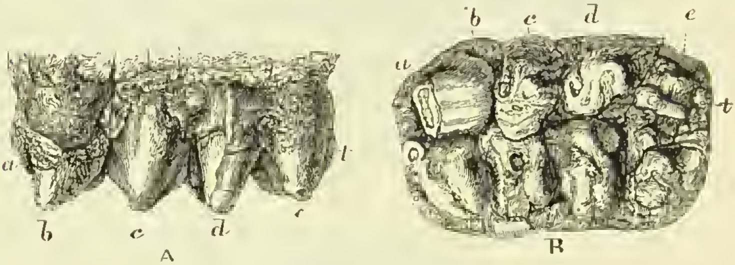
(¹) Skull of Dinotherium. (After Owen.)

downward pointing tusks were about 2 feet in length ; as, however, tusks of only half this length were found in some jaws of identical dimensions and in other respects similar, it is believed that the male Dinotherium had larger tusks than the female. The molar teeth, much like those of a tapir, need not detain us.

$$i\,\frac{0}{1}\;c\,\frac{0}{0}\;pm\,\frac{2}{2}\;m\,\frac{3}{3}.$$

The succession was vertical, as in other mammals, and it had dm $\frac{3}{3}$.

Fig. 200 ([1]).



But the Dinotherium, Mastodon, and Elephant present us with a very instructive series of modifications in which we see how the excessively complex grinder of the Indian elephant was attained to by degrees.

The molar of the Dinotherium resembles that of a tapir somewhat ; it has not any very great exaggeration of its cusps, and does not deviate very widely from the form of many other mammalian teeth ; the premolars and molars all have two ridges, with the exception of the last milk molar and the first true molar, which have three.

The tooth of Mastodon has its cusps or ridges more numerous and more pronounced, as is seen in the accompanying figure.

Other Mastodons have more numerous ridges upon the teeth, and the African elephant has as many as ten upon its

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(1) Molar tooth of Mastodon.

FIG. 201 (1).

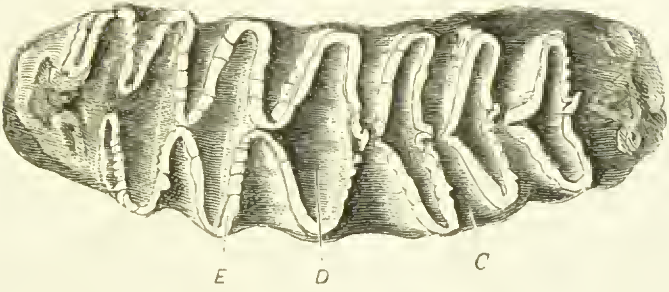


FIG. 202 (2).

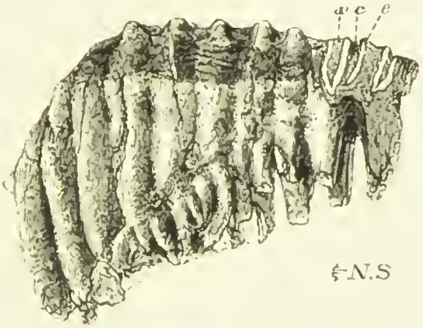
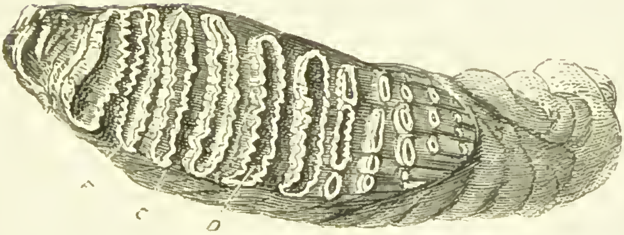


FIG. 203 (3).



(1) Molar of African elephant. *E.* Enamel. *D.* Dentine. *C.* Cementum.

(2) Molar tooth of African elephant, showing the form of its roots, &c. *a.* Dentine. *c.* Cementum. *e.* Enamel.

(3) Molar tooth of an Asiatic elephant, showing the transverse plates of dentine bordered by enamel.

last or larger molar, although in it the ridges are individually wide and strongly pronounced.

In the Indian elephant the ridges or plates are still more numerous, the roots very inconspicuous, and the whole formed into a solid block by cementum.

The gradual increase in complexity in the "ridge formula" (or number of ridges in each tooth), of the molars, is well seen in the following table, from Professor Flower's Hunterian lecture ("Nature," March 2, 1876); it is a corrected table taken from Dr. Falconer's "Palæontological Memoirs."

	Milk Molars.			True Molars.			Total.
	I.	II.	III.	I.	II.	III.	
Dinotherium giganteum . . .	1	2	3	3	2	2	13
Mastodon (Trilophodon americanus)	1	2	3	3	3	4	16
,, (Tetralophodon) arvernensis	2	3	4	4	4	5	22
,, (Pentalophodon) sivalensis .	3	4	5	5	5	6	28
Elephas (Stegodon) insignis . .	2	5	7	7	8	10	39
,, (Loxodon) africanus . .	3	6	7	7	8	10	41
,, ,, meridionalis . .	3	6	8	8	9	12	46
,, (Euelephas) antiquus . .	3	6	10	10	12	16	57
,, ,, primigenius .	4	8	12	12	16	24	76
,, ,, indicus . .	4	8	12	12	16	24	76

Some variability exists in the number of ridges, especially when they are very numerous, but the above may be taken as averages: and some species intermediate in the "ridge formula" have been since discovered; thus M. Pentelici and M. Andium bridge the distinction between Trilophodon and Tetralophodon, and Elephas melitensis comes between Loxodon and Euelephas (Flower).

It remains to describe, somewhat more in detail, the structure of an elephant's tooth, and this has been deferred till the last, because it can be the more easily understood when the manner of its origin has been mastered. In the Mastodon the molar consists of a crown with strong cusps standing apart, and with marked roots; in the African elephant that part which consists of cusps has become the greater bulk of the tooth, the roots are comparatively insignificant, and the interspaces of the cusps are filled up with cementum. The molar of the Indian elephant consists of a larger number of yet more elongated and flattened cusps, so that the greater part of the tooth is made up of these flattened plates, fused together with cementum, and so forming a strong and solid mass; the roots are comparatively inconspicuous. Thus we have a process of evolution going on exactly as in other Ungulata: the rooted and distinctly cuspid tooth of the Mastodon has but little coronal cement, whilst as the cusps and ridges deepen, and the tooth becomes more of hypsodont type, at the same time the ridges become more numerous, and the coronal cement increases in quantity so as to fuse it into a solid block.

When the tooth is a little worn each plate consists of an area of dentine surrounded by enamel. The interspaces of the series of plates are wholly filled up by cementum; the summits of each plate were originally mammillated, and divided up into more numerous blunt processes than the corresponding parts of the tooth of a Mastodon; so when the tooth comes into use the rounded tips are soon worn off, and the grinding surface of the tooth then consists of narrow transverse bands of dentine, surrounded by enamel, and of cementum in their interspaces. The difference in hardness between these three tissues preserves a constant rough surface, owing to their unequal rate of wear. In their wild condition elephants eat trees with succulent juicy stems, and oftentimes grass torn up by the roots, from which they roughly shake out the adherent earth. In confinement, the food containing less that is gritty, the teeth become polished by working against one another, but the rate of wear is insufficient to keep their surfaces rough; for the softer cementum does not get worn down in the interspaces of the plates of dentine and enamel, but remains on a level with them.

The celebrated elephant "Jumbo" suffered from insufficient wear of his teeth, so that the earlier ones being insufficiently worn were not got rid of at the proper time, and interfered with the normal development of their successors.

Great though the size of the Proboscideans be, they have some points of affinity with the Rodents in the great development of the incisors, in the vacant interval between these and the molar teeth, and, as was pointed out by the late Professor Rolleston, in the enamel of the elephant's molar having, in its inner portions, a pattern produced by the decussation of the prisms, which is very similar to that described by my father as characteristic of all the Rodents save the Leporidæ (Hares), and Hystricidæ (Porcupines).

There remain to be considered some of the strange forms of late years discovered in America, and of which the classification is as yet provisional.

EXTINCT UNGULATES.

SUB-ORDER AMBLYPODA (DINOCERATA).

In the same region which yielded the toothed birds (Eocene formations of Wyoming), the remains of many huge animals have been discovered, for which new orders have been proposed by Professor Marsh ("American Journal of Science and Art," 1876), it being impossible to classify them under any existing order. The Dinocerata were creatures nearly as large as elephants, and presenting some sort of resemblance to them in general form; they were remarkable for the relative smallness of their brains, which could apparently have been drawn through the canal of the vertebral column. They present points of resemblance to the Perissodactyle Ungulata, and also to the Proboscidea, to which they were at first referred, though their affinities are rather with the former.

The dental formula was

$$i\,\frac{0}{3}\;c\,\frac{1}{1}\;prm\,\frac{3}{3}\;m\,\frac{3}{3}.$$

In Professor Marsh's words, "The superior canines are long, decurved, trenchant tusks. They are covered with enamel, and their fangs extend upwards into the base of the maxillary horn-core. There is some evidence that these tusks were smaller in the females. Behind the canines there is a moderate diastema. The molar teeth are very small. The crowns of the superior molars are formed of two transverse crests, separated externally, and meeting at their inner extremity. The first true molar is smaller in this specimen than the two preceding premolars. The last upper molar is much the largest of the series.

"The lower jaw in **Dinoceras** is as remarkable as the skull. Its most peculiar features are the posterior direction of the condyles, hitherto unknown in Ungulata, and a massive decurved process on each ramus extending downward and outward below the diastema.

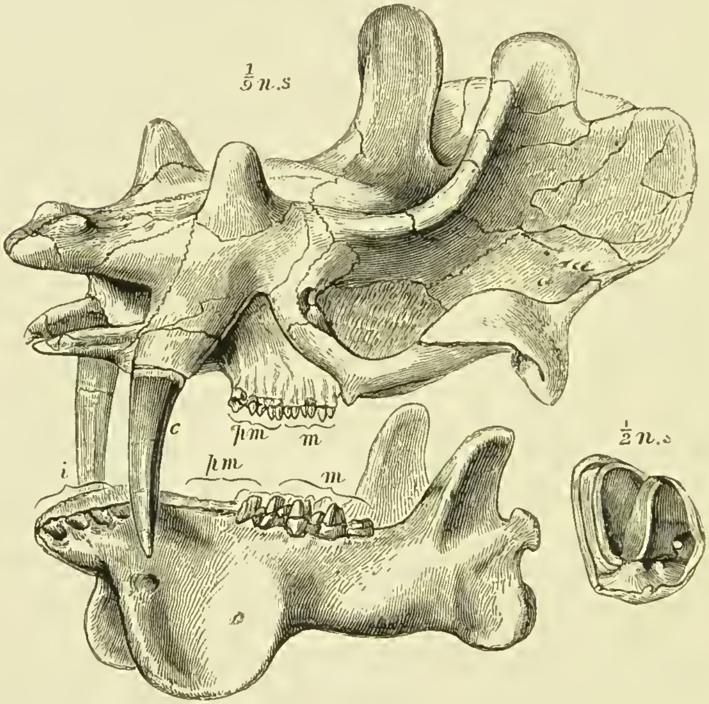
"The position of the condyles was necessitated by the long upper tusks, as, with the ordinary ungulate articulation, the mouth could not have been fully opened. This low position of the condyle, but little above the line of the teeth, is a noteworthy character. The long pendant processes were apparently to protect the tusks, which otherwise would be very liable to be broken. Indications of similar processes are seen in Smilodon and other Carnivores with long upper canines. With the exception of these processes the lower jaw of Dinoceras is small and slender. The symphysis is completely ossified. The six incisors were contiguous, and all directed well forward. Just behind these, and not separated from them, were the small canines, which had a similar direction. The crowns of the large molars have transverse crests, and the last of the series is the largest."

It would appear possible that the eminences shown in the figure, and spoken of as "maxillary horn-cores," may be merely the extended sockets of the teeth, which would otherwise have had an implantation inadequate to their length; they are, however, described as solid, except at their bases, where they are perforated for the root of the canine tusk, which would look as though they were truly horn-cores; moreover the Brontotheridæ had horn-cores equally peculiar in position (*i.e.*, on the maxillary bones).

Tinoceras, another genus, had a very longer and slender canine, also protected when the mouth was closed by a downward prolongation of the lower jaw as in Dinoceras.

Another extraordinary creature discovered by Marsh is

Fig. 204 (¹).



Protoceras. It appears, according to Osborn and Wortman, to have affinities with the Pecora and Tragulina, and belongs to the Artiodactyle section of the Ungulate order.

It had no upper incisors, but was possessed of large trihedral canines in the upper jaw; the lower incisors and canines ranged together as in ruminants, and were of

(¹) Upper and lower jaws of Dinoceras (Marsh).

spatula-like shape; the molar teeth were selenodont and brachydont.

The female was possessed of canines, but they were only half the size of those of the male, and the skull of the female was smooth, though that of the male fairly bristled with ten bony prominences, upon which, however, there appear not to have been any true horns.

Although it was really quite distinct from the Dinocerata, being an Artiodactyle, the general aspect of the skull, with its prominences and its dentition seen in side view, much resembled Dinoceras, thus affording a striking case of "parallelism."

SUB-ORDER CONDYLARTHRA.

These were smaller and more generalised Ungulates, with affinities both with the Artiodactyle and the Perissodactyle groups. They usually had the full mammalian dental formula, and the molars were brachydont, and usually bunodont. The premolars were simpler than the molars, and tritubercular teeth were common in the group.

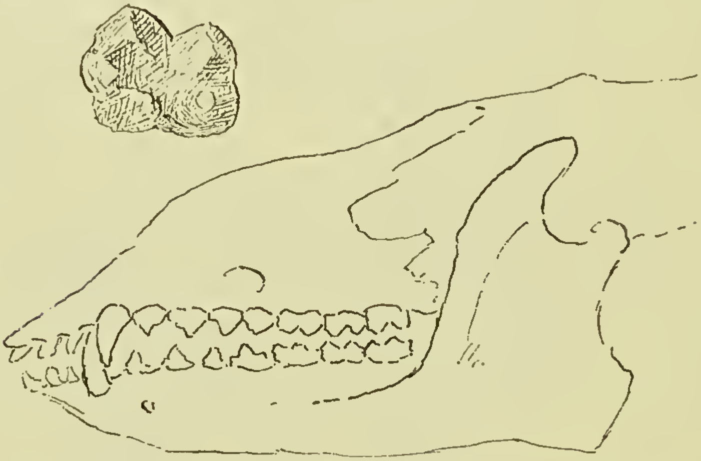
Cope has suggested that the ancestors of the Lemurs are to be found in this group, whilst the genus Phenacodus is perhaps the source whence the line of modification ending in the Horse has been derived. It also comes near to the Hyracoidea, so that it is a highly generalised form, and Cope regards it as the ancestor of all Ungulates, though not of all placental mammals, inasmuch as its molars were already quadritubercular. But he points out that one has to go back but a short time to find its tritubercular ancestors, so that it is but a little way from what may be regarded as the common stock.

Phenacodus had a dental formula—

$$i\frac{3}{3}\ c\frac{1}{1}\ pm\frac{4}{4}\ m\frac{3}{3}.$$

The incisors were somewhat expanded transversely, and the canines were not very large, the inferior incisors being directed somewhat obliquely forwards, and the front part of the jaw was weak. The premolars stand a little apart, the first having only one root and a simple crown, the others bearing an internal lobe and two external cusps. The upper molars had four cusps, two external and two internal, with in addition two slight intermediate cusps and a narrow cingulum. The lower molars had four cusps like those of the upper, and a small odd one behind.

FIG. 205 (1).



The small isolated cusps which occur between the principal ones in later forms develop into cross ridges connecting the outer and inner cusps, and so produce a lophodont molar.

TOXODONTIA.

The existing Ungulate animals form only a small proportion of those once peopling the earth, and many extinct forms have been discovered, which while forming affinities with the Ungulata, can yet hardly be classified under any existing order. For example, **Toxodon**, a creature equalling the Hippopotamus in size, which was discovered by Mr. Darwin in late Tertiary deposits of South America, has a dentition recalling in some respects the Bruta, in others the Rodents.

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(1) Phenacodus primævus (half nat. size). (After Cope.) The grinding surface of a lower molar is represented above.

Its dental formula was—

$$\mathrm{i}\,\frac{2}{2}\ \mathrm{c}\,\frac{?0}{1}\ \mathrm{p}\,\frac{4}{3}\ \mathrm{m}\,\frac{3}{3},$$

the median pair of upper incisors being small, the outer exceedingly large, with persistent pulps, and long curved sockets, extending back to the region of the molars, just as in existing Rodents.

In the lower jaw there were three pairs of incisors, subequal in size, and growing from persistent pulps; they resemble the incisors of Rodents in having a partial investment with enamel, but differ from them in being prismatic in section, and in having the enamel disposed on two sides of the prism.

The molars were also very remarkable; they grew from persistent pulps, and had curved sockets, but the curvature of these was in the reverse direction to that which obtains in Rodents, *i.e.*, the convexity was outwards, and the apices of their roots almost met in the middle line of the palate; it was this peculiarity that suggested the name.

Another peculiarity in the molar teeth, in which they stand quite alone, is that, like the incisors, they have a partial investment with enamel; those referred to the premolar series having it confined to their outer surfaces, while the three back teeth of the molar series had a plate also laid on to their inner surfaces; there were seven back teeth above, and six below.

In the interval between the incisor and molar series canines have been found in the lower jaw; they were sharp-edged, and had a partial distribution of enamel over their surface. In an upper jaw alveoli for canines were found, but the teeth themselves are not known.

Another animal from the same locality (Mesotherium or

Typotherium) had somewhat similar characters, though it was not nearly so large: it had

$$i\,\frac{1}{2}\;c\,\frac{0}{0}\;pm\,\frac{2}{1}\;m\,\frac{3}{3},$$

the incisors (of persistent growth) standing apart from the premolar and molar series just as in the Rodents. It is remarkable that this animal, which possessed a clavicle, in its skeleton also shows on the one hand generalised Ungulate characters, and in others resemblances to the Rodents.

TILLODONTIA.

This, yet another new order, comprising several genera, has been proposed by Professor Marsh to receive some Wyoming fossil remains, which, though not amongst the biggest, are "amongst the most remarkable yet discovered in American strata, and seem to combine characters of several distinct groups, viz.: Carnivora, Ungulata, and Rodentia." In **Tillotherium** (Marsh), the type of the order, the skull has the same general form as in the bear, but in its structure resembles that of the Ungulata. Its molar teeth are of the Ungulate type, the canines are small, and in each jaw there is a pair of large scalpriform incisors, faced with enamel, and growing from persistent pulps, as in the Rodents. The hinder pair of incisors are small, and have not persistent pulps, and it is pointed out by Wortman that the greatly developed incisors are the second pair, the first and third that are disappearing.

Esthonyx (Cope), an Eocene mammal with a dentition roughly resembling that of a gigantic Shrew, foreshadows it, having $i\,\frac{2}{3}$, of which $\overline{i_3}$ is extremely reduced, while $\overline{i_2}$ is enlarged and its enamel confined to its anterior and external aspects; $\underline{i_1}$ is absent, $\underline{i_2}$ enlarged, with no enamel on its back, but none of these teeth grow from persistent pulps.

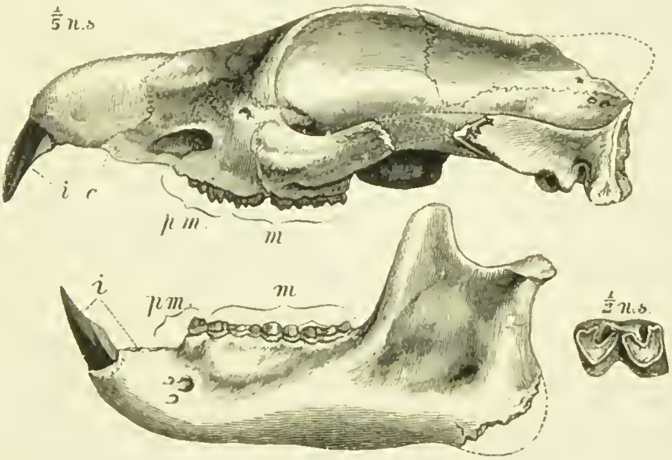
The adult dentition of Tillotherium is as follows—

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;pm\,\frac{3}{2}\;m\,\frac{3}{3}.$$

"There are two distinct families, *Tillotheridæ* (perhaps identical with *Anchippodontidæ*), in which the large incisors grew from persistent pulps, while the molars had roots; and the *Stylinodontidæ*, in which all the teeth have persistent pulps."

One genus (Dryptodon), known only by the lower jaw, had six teeth, described as "clearly incisors," the two inner pairs of which are small and cylindrical, the outer of enormous size, faced in front only with enamel, and with persistent pulps carried back under the premolars.

Fig. 206 (¹).



Whilst Professor Flower endorses Professor Marsh's view that Tillodonts have Ungulate affinities and resemblances to Rodents also, this is disputed by Dr. Wortman ("Amer. Syst. Dental Surgery," Art. Teeth of Vertebrates), who says that he fails to discover any traces of Ungulate relationship, and he prefers to refer them to those generalised forms with Insectivorous affinities which Professor Cope groups as Bunotheria. The adaptive character of incisors faced with enamel and of persistent growth he would appear to consider as not going far towards establishing more than a superficial

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(¹) Upper and lower jaws of Tillotherium (Marsh).

resemblance to Rodentia. He holds that Tillodonts are probably descendants of Esthonyx, itself allied to the Shrews, and that they may also have given origin to the Toxodonts.

THE TEETH OF RODENTIA.

The animals belonging to this order, which is sharply defined, are scattered almost all over the world. The island of Madagascar is, however, remarkable for being almost without indigenous Rodents, as is the case also with Australia, two facts which are of no small interest to the student of odontology.

For in each of these areas, out of the creatures which are there (in the one Lemurs, in the other Marsupials), there has arisen a form so modified as to mimic and take the place of the true Rodents, viz., the Chiromys in Madagascar, and the Wombat in Australia.

In past times, however, a large number of animals, widely apart from one another in their affinities, have more or less approximated to the characteristics of rodent dentition, and as this adaptive resemblance would give to them advantages in getting access to food which was denied to animals with relatively blunt and weak front teeth, it is not unlikely that some of these may have left descendants, and that hence the existing Rodents may have sprung from more than one stock.

The species of Rodents are exceedingly numerous, and the great majority of them are of small size; the aquatic Capybara is far the largest of recent Rodents.

An average Rodent dentition would be—

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{1}{1}\text{ or }\frac{0}{0}\;m\,\frac{3}{3};$$

as extremes the **Hare** has—

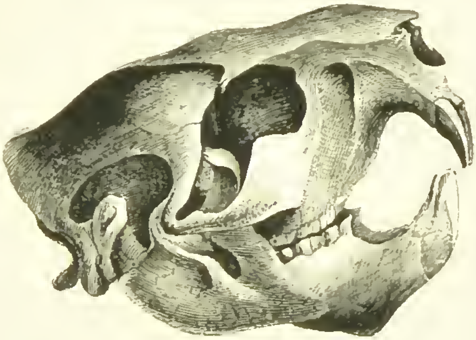
$$i\,\frac{2}{1}\;c\,\frac{0}{0}\;pm\,\frac{3}{2}\;m\,\frac{3}{3},$$

and Hydromys—

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{0}{0}\;m\,\frac{2}{2}.$$

In general features the dentitions of the numerous species comprising this order are very uniform; the incisors (save in the hares and rabbits, in which there is an accessory small pair immediately behind the large ones) are reduced to four in number, are of very large size, and grow from persistent pulps. The jaws for some little distance behind the incisors are devoid of teeth, while beyond the interval the back teeth, generally not more than four in number, are arranged in lines which diverge slightly as they pass backward. The large scalpriform, or chisel-like incisors, extend far back into the jaws, and are much curved, the upper incisors, in the words of Professor Owen, forming a larger segment of a smaller circle than the lower, which are less curved. The length and curvature of these incisors relieve from direct pressure their growing pulps, which come to be situated far back in the jaw, the open end of the lower incisor, for example, being in many species actually behind the last of the molar teeth. The nerve going to supply the persistent pulps is of very large size, and, owing to the open end of the tooth having formerly occupied a more anterior position in the jaw, runs forward beneath the tooth, and then bends abruptly backwards to reach the tooth-pulp. In many Rodents the enamel of the

FIG. 207 (1).



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(1) Side view of skull of a rodent, giving a general idea of the dentition of the order.

front of the large incisors is stained of a deep orange colour; this colour is situated in the substance of the enamel itself.

The scalpriform incisors terminate by cutting edges, the sharpness of which is constantly maintained by the peculiar disposition of the tissues of the tooth.

The investment of enamel, instead of being continued round the whole circumference of the tooth, is confined to its anterior and lateral surfaces, on the former of which it is thickest.

It is, however, stated that the enamel organ is continued round the roots, so that the connective tissue bundles by which attachment to the cementum is made, have to grow through it to take their hold. (V. Brunn.)

It is said by Hilgendorff ("Berlin Akad. d. Wiss. Monatsbericht," 1865), that the incisors of hares differ from those of all other Rodents in having enamel all round them, although it is very thin at the back. I have not been able to satisfy myself that the thin clear layer at the back of the tooth is enamel, and am disposed to regard it as cementum, the more so as it seems to be continued a little way upon the enamel, and in very young teeth the large cells of the enamel organ are confined to the anterior surface (1).

When a Rodent incisor has been exposed to wear, the anterior layer of enamel is left projecting beyond the level of the dentine, and this arrangement results in a very sharp edge being constantly maintained. The dentine also is harder near to the front of the tooth than towards the back of the tooth. It is said that no enamel was ever present on the tip of the incisor.

A thin external coat of cement is found upon the back of the tooth, but is not continued far over the face of the enamel. But in the Marsupial wombat this layer of cement is continued over the whole anterior surface of the scalpriform incisors.

Behind the scalpriform incisors in all Rodents there comes a wide gap, there being no canines and but few premolars; this gap leaves the growing incisors free scope in use.

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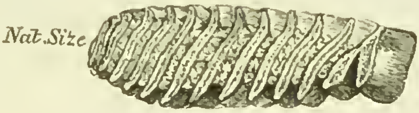
(1) Cf. E. G. Betts, "Trans. Odontological Society," May, 1884.

The grinding teeth are not very numerous; the mouse family have usually $\frac{3}{3}$; the porcupines have constantly $\frac{4}{4}$, and the hares $\frac{6}{5}$; the Australian water-rat (Hydromys) is altogether exceptional in having so few as $\frac{2}{2}$. Observation has established that the last three of the teeth are always true molars, and that when there are more than three, the rest are premolars.

Fig. 208 (1).



A good deal of diversity exists in the premolar and molar teeth; in Rodents of mixed diet, such as the common rat, the back teeth are coated over the crown with enamel, which nowhere forms deep folds, and have distinct roots, *i.e.*, are not of persistent growth; the molars of the rats have some sort of resemblance to minute human molars. In aged specimens the enamel is consequently worn off the grinding surface of the crown, which comes to be an area of dentine, surrounded by a ring of enamel.

But in those whose food is of a more refractory nature, the molars, like the incisors, grow from persistent pulps (as is exemplified in the Capybara here figured), and their working surfaces are kept constantly rough by the enamel dipping in deeply from the side of the tooth, as may also be seen in the common water-rat. The inflection of enamel may be so deep as to divide the areas of dentine completely up, the result being a tooth like that of the Capybara, which is composed of a series of plates of dentine, or "denticles," surrounded by layers of enamel, and all fused together by the cementum. The result of this disposition of the structures is that the working surface is made up of enamel, dentine, and cementum, three tissues of different hardness, which wear down at different rates, and so maintain its roughness. Various intermediate forms of the molar teeth are met with; thus, there are some in which complexity of the surface is maintained by folds of enamel dipping in for a little distance, but which, nevertheless, after a time form roots and cease to grow. In general terms it may be said of the Rodents just as of Ungulata, that the brachydont bunodont type is the older, and that the laminated hypsodont type is of later acquisition. And, as is pointed out by Forsyth Major ("Proc. Zool. Soc.," 1893), the young,

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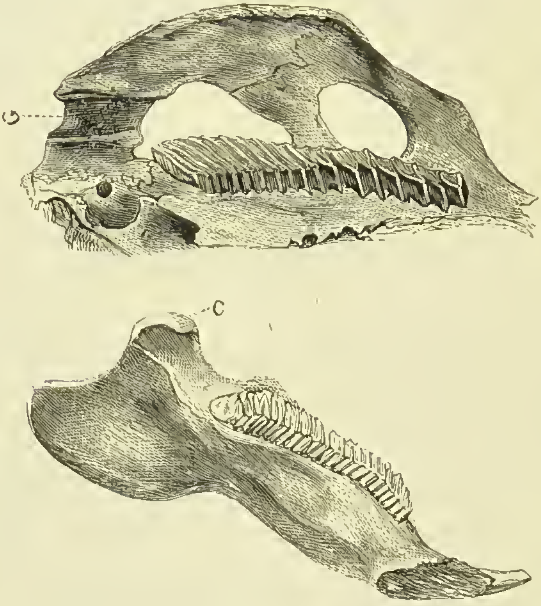
(1) Molar of Capybara, showing the transverse plates of dentine and enamel united to one another by cementum.

Fig. 209 (1).



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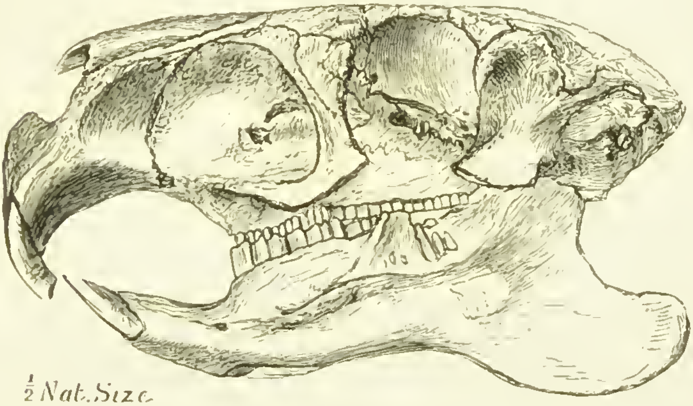
(1) Condyle and glenoid cavity of the Capybara, showing their longitudinal direction.

unworn, laminated hypsodont molar is at first tuberculated or bunodont, and the brachydont tubercular molar, when worn down, partakes more or less completely of the laminated pattern on its grinding surface. When the molar teeth grow from persistent pulps, they are always curved, like the incisors, with the effect of relieving their pulps from direct pressure during mastication; and the last remains of the pulps are converted into secondary or osteo-dentine, which thus forms the central axis of the incisors, or molars, as the case may be. In this tissue vascular tracts sometimes exist, but it is altogether small in amount, the formation of true dentine going on till the pulp at that particular point is almost obliterated.

Fig. 210 (¹).



½ Nat. Size.

As has already been mentioned, when the molar series consists of more than three teeth, those anterior to the three true molars are premolars, but they do not differ materially in size or form from the true molars.

The forms of the condyle and of the glenoid cavity in Rodents are characteristic; they are much elongated in an antero-posterior direction, so that the range of backward and forward motion, made use of in gnawing, is very considerable. The Leporidæ are exceptional in having more

(¹) Cranium of Capybara.

lateral play than most Rodents. And the power of the teeth is marvellous; rats will sometimes gnaw holes in water-pipes, or in gas-pipes, in which they have heard water bubbling.

The general character of a Rodent's dentition may be illustrated by a description of that of the **Capybara.**

The incisor teeth are squarish. They are wider than they are deep, and are slightly grooved on their anterior surface.

There are four grinding teeth on each side, of which the first three are small, and with few cross plates of dentine and enamel, but the fourth is a very complex tooth, with twelve or more such plates, which are fused into a solid mass by cementum.

This tooth being one of persistent growth, there is no common pulp cavity, but each plate has its own.

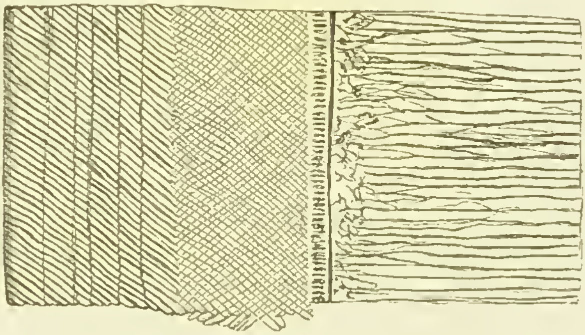
It has already been mentioned (p. 184) that the dentinal tubes at that part of the Rodent's incisor which has come into use are much smaller than those near to its growing base, thereby proving that they have undergone a diminution in calibre at a time subsequent to their original formation. Near to the surface actually in wear they become cut off from the pulp cavity by the conversion of what remains of the pulp into a laminated granular mass, so that the dentine exposed on the surface of a Rodent's tooth must be devoid of sensitiveness, and the contents of the dentinal tubes must have presumably undergone some change. But what the nature of the change in the contents of dentinal tubes which have ceased to be in continuity with a vascular living pulp may be, there are, so far as I know, no observations to indicate.

As was shown by my father ("Phil. Trans.," 1850), the enamel of Rodents is peculiar, and some little diversity in the arrangement of the prisms exists in different families of the order, their character being in many cases so marked, that it is often possible to correctly refer a tooth to a particular family of Rodents after simple inspection of its enamel.

In general terms it may be said that the enamel is divided into two portions, an outer and an inner portion (this is true of all save the hares and rabbits), and that the enamel prisms pursue different courses in these two portions.

Thus, in the enamel of the beaver, in the inner half, nearest to the dentine, the prisms of contiguous layers, as seen in an oblique tranverse section, cross each other at right angles, whereas in the outer portion they are all parallel with one another, presenting, however, the peculiarity of not running straight on to the surface at right angles to it, but inclining to the middle line of the skull.

Fig. 211 (¹).



In the genera Sciurus, Pteromys, Tamias, and Spermophilus the enamel fibres, as seen in longitudinal section, start from the dentine at right angles to its surface; in Castor they incline upwards at an angle of 60°, but preserve the distinction between the outer and inner layers very distinctly.

In the Muridæ the decussation of the layers in the inner part, and their parallelism in the outer part of the enamel are also found, but in addition to this the borders of the individual prisms are slightly serrated, the serrations of contiguous fibres interlocking.

In the porcupine sub-order the fibres of the inner portion

(¹) Transverse oblique section of an incisor of a beaver (Castor fiber). The enamel prisms of superimposed layers cross each other at right angles in the inner portion of the enamel, but all become parallel in the outer. For fuller description of this figure see p. 16.

of the enamel pursue a serpentine course, nevertheless showing indications of a division into layers; they become parallel in the outer portions as in other Rodents. Small interspaces are found amongst the enamel fibres of the porcupines.

In the hares (Leporidæ) the lamelliform arrangement, and the division into outer and inner layers, alike disappear.

The peculiarities in the disposition of the enamel fibres, which are so marked in the incisors, do not generally exist in the molars of the same species, except when these are of continuous growth.

Many minor differences in the arrangement of the enamel prisms exist, for a description of which I must refer the reader to the original paper, but in general terms it may be said that the "enamel lamellæ have a different and distinctive character in each of the larger groups, and that the variety of structure is constant throughout the members of the same group; we may take, for example, the Sciuridæ, the Muridæ, and the Hystricidæ, in each of which the structure of the enamel is different; and in each is highly distinctive." And further, that the varieties in the structure of the dental tissue, so far as they are known, with a few isolated exceptions, justify and accord with the classification of the members of the order usually given.

It is stated by von Ebner that tubes exist in the enamel of hares and of Cavia, but that they do not communicate with the dentinal tubes. There is, however, no doubt that in Jerboa the tubes in the enamel are in continuity with those of the dentine.

The milk dentitions of the Rodent have been investigated by a number of observers, with rather discrepant results. At all events, we may say that the extent to which the milk teeth are developed varies much.

It has already been mentioned that in the hares and rabbits there are four incisors in the upper jaw, a small and apparently functionless pair being placed close behind the large rodent incisors; but in very young specimens there are six incisors, of which the one pair are soon lost.

Professor Huxley ("Nature," vol. 23, p. 228) wrote "The deciduous molars and the posterior deciduous upper incisors of the rabbit have been long known. But I have recently found that unborn rabbits possess, in addition, two anterior upper and two lower deciduous incisors. Both are simple conical teeth, the sacs of which are merely embedded in the gum. The upper is not more than one-hundredth of an inch long, the lower rather larger. It would be interesting to examine fœtal guinea-pigs in relation to this point; at present they are known to possess only the hindmost deciduous molars, so far agreeing with the Marsupials." These additional teeth he rightly interpreted as being milk teeth, and not as representatives of an additional pair of incisors.

His observation has been confirmed by Pouchet and Chabry, Freund, Woodward and others. The latter observer has re-investigated them, and finds ("Anat. Anzeig.," 1894)

that $\frac{\text{di. 1}}{\text{di. 1}}$ never cut the gum and are absorbed in uteri.

di $\frac{2}{0}$ is functional, and is shed about the third week after birth.

dpm $\frac{3}{2}$ are functional, and are shed about the same period as the last.

The squirrel also has milk incisors (Freund); there are three rudiments described by that author, which Woodward, as it appears to me with good reason, interprets as a milk incisor, as a vestigial milk incisor representing the second incisors of the hares and rabbits, and as a third incisor (Freund regarding the last as a canine).

Woodward describes a pair of minute calcified rudiments in the mouse, though their presence is not quite constant. Thus the squirrel, the rabbit, and the mouse present three stages in the reduction of the vestigial milk incisors. In other rodents no milk teeth are known in the front of the mouth.

In the molar region Cuvier discovered a single milk premolar in the upper and lower jaws of the guinea-pig, which never becomes functional.

Mr. Waterhouse ("Nat. Hist. of Mammalia—Rodents," p. 4), has found the milk molars still in place in the skull of a half-grown beaver; while in the hares they are shed about the eighteenth day after birth, and in the guinea-pig disappear before birth.

Hares and rabbits have six milk molars in the upper and four in the lower jaw, which come into use, but differ from their successors in forming definite roots, and not growing from persistent pulps.

Other Rodents, such as the rat, which has only three teeth of the molar series on each side, and the Australian water-rat (Hydromys) have no known milk teeth, and are hence perhaps truly Monophyodont.

Milk premolars have been described in the hare and rabbits, in Castor, Dasyproeta, Ctenodactylus, Hystrix, Atherina, and Erethizon, so that it is probable that further search will reveal traces of others. In Atherina, a brush-tailed porcupine, there is a single well-developed and functional milk premolar on each side of both jaws.

Rodents are fairly well represented in Eocene Tertiary deposits, but their ancestry is by no means clear. Professor Cope considers that the Tillodonta (see p. 446) may have been the ancestors of existing rodents, and gives ("Factors of Evolution," p. 329) an instructive series of reduction of certain incisors, and hypertrophy of others in Esthonyx, Psittacotherium, Calamodon, and Anchippodus, in which one pair of very rodent-like incisors remain in the lower jaw. He holds with Ryder that continued severe use has resulted in hypertrophy of these teeth, and that the backward and forward excursions of the jaw have led to the disappearance of the post-glenoid process in the articulation, allowing of the very posterior position of the lower jaw characteristic of rodents.

Forsyth Major (On Miocene Squirrels, "Proc. Zool. Soc.," 1893) states that the investigation of early rodents lends no support to the tritubercular theory, but that a brachydont bunodont molar is obviously the more primitive type among them, and that the more brachydont the tooth the more it is multitubercular. He holds that in the molars of all mammals a tendency to reduction and simplification, which proceeds from the inner side outwards in the upper jaw and from the outer side inwards in the lower jaw, is traceable, and that the true tritubercular molar having been arrived at in this way, is not a primitive, but a specialised type. (Cf. p. 452.)

THE TEETH OF CARNIVORA.

The animals grouped together under the name of Carnivora are divided into two sections, the Aquatic and the Terrestrial Carnivora.

The terrestrial Carnivora were formerly classed as "digitigrade" and "plantigrade," a classification exceedingly inconvenient. as it left the greater number of the animals to be classified in the debatable ground between the two extreme types. As a linear classification is impossible, they are now grouped around three centres: the Æluroidea, or cat-like; the Cynoidea, or dog-like; and the Arctoidea, or bear-like Carnivora: and, instead of taking the Felidæ, or Cats, as the type of the group, it is generally considered that the Dog tribe are the most generalised form, and that the Cats are an extreme modification in one direction, the Bears in another.

The Cynoidea comprise the Dog, and its immediate allies, the Wolves and Foxes.

The Æluroidea, or Cat-like Carnivora, comprise the Viverridæ (Civets), Hyænas, and Cats.

The Arctoidea, or Bear-like Carnivora, comprise the Mustelidæ (Weasels), Procyonidæ (Racoons), and the true Bears.

This arrangement is a very convenient one, so far as recent Carnivora go, but it breaks down when the extinct forms are included, the Arctoidea having perhaps been derived, some from the Canidæ, others from the Viverridæ.

The order Carnivora is a very natural one, and its name is, upon the whole, fairly descriptive of the habits of the majority of its members: though there are some creatures included in it which are mixed feeders, and others which are purely vegetarian.

In this order, just as in the Ungulata, the rich North American fossil fauna has furnished ancestral forms (Creodonts of Cope), whence modern Carnivora and also Insectivora may have diverged, just as the Ungulates have diverged from the Condylarthra.

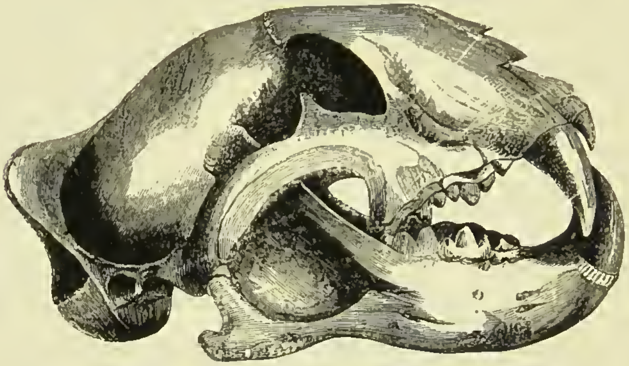
In carnivorous animals one tooth on each side of both upper and lower jaws is of considerable length, is sharply pointed, and is called a canine; the upper canine is separated by an interval from the incisors, the lower canine being received into the vacant space or "diastema" so formed.

The incisors are short, almost always six in number, and stand nearly in a straight line, transversely across the front of the jaw, the outermost upper incisor being sometimes large and pointed, so as to be like a small canine.

The incisors and canines may, on the whole, be said to be tolerably uniform throughout the order, but the variations in the premolar and molar teeth are both numerous and interesting.

In the most purely carnivorous members of the order, the Felidæ, the true molars are reduced to a minimum, and the back teeth are thin edged, "sectorial" teeth; in the Bears, on the other hand, some of which are purely herbivorous, the molars are little short of a full typical mammalian number, and are furnished with obtuse and broad grinding surfaces.

Fig. 212 (1).



The accompanying figure will serve to give the general aspect of the teeth and jaws of a typically carnivorous animal, and to show the great development of the processes for the attachment of muscles, and the stout wide arch of the zygoma.

To a particular tooth in the upper jaw, and to its antagonist in the lower jaw, Cuvier gave the name of "carnassial;" these, conspicuous in the true flesh-feeders, become less differentiated in the Arctoidea or bear-like Carnivora, and in the bears themselves are indistinguishable from the other teeth, save by a determination of their homologies by a process of comparison with the teeth of intermediate forms.

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(1) Side view of the cranium of a tiger, with the mouth slightly opened to show the relative position of the great canines.

The sectorial or carnassial tooth in the upper jaw is always the fourth premolar; its crown is divisible into two parts, the one a thin sharp-edged blade, which runs in an antero-posterior direction, and is more or less divided by one or two notches into a corresponding number of cusps; the other part, the "tubercle," is a shorter and blunter cusp, and supported upon a distinct inner root situated at the inner side of the anterior end of the blade. (See Figs. 213 and 214.) In those which are most purely flesh-feeders, the "blade" is well developed, and the tubercle of small size; an increase in the tubercular character of the tooth is traceable through those genera which are mixed feeders.

Thus in the bears the tubercle is said to be highly developed; but it is to be noted that the large flattened inner portion of the bear's sectorial tooth is in a more posterior position than the tubercle of a cat's sectorial, and is not supported upon any separate root.

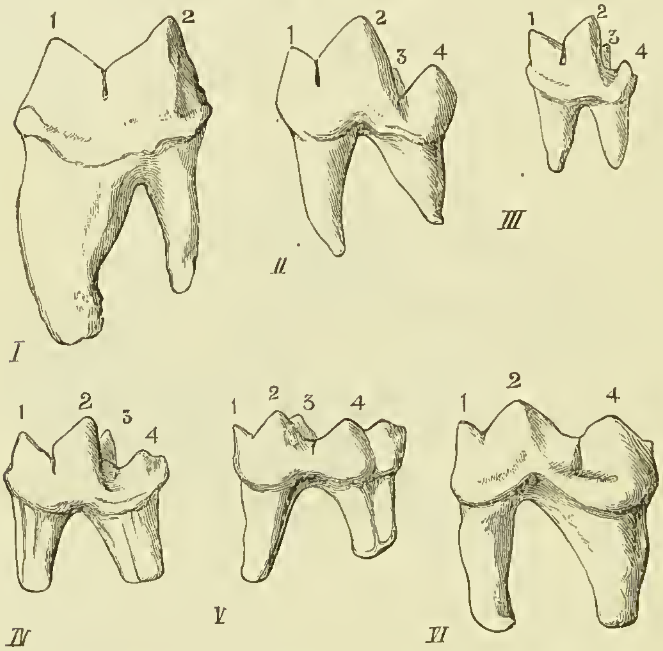
The lower tooth which antagonises the upper carnassial, passing a little behind it, is the first true molar; in the Felidæ it consists solely of the blade, which is divided into two large cusps, behind which is a very small and rudimentary third division (which in the Hyænidæ, for example, is of conspicuous dimensions). In existing Carnivora but one "sectorial" tooth is to be found on each side of the jaws, but in the Hyænodon, which had the full number of forty-four teeth, and in some other extinct Tertiary mammals, there were more teeth partaking of this character.

When the blade of the upper carnassial tooth consists of only two cusps, as in the Dog, these are the paracone and metacone of the primitive triangle—the inner tubercle supported on a special root is the protocone.

The blade of the lower carnassial molar consists apparently of the paraconid in front and protoconid behind, the metaconid or postero-internal cusps having gone; according to the tritubercular theory the first change from the primitive trituberculism was the addition of a low heel to the lower teeth, thus forming the tuberculo-sectorial tooth, which, in the most specialised forms, such as the Felidæ, has disappeared again. It is pointed out by

Marett Tims ("Journal Linnæan Soc.," 1896) that cusp identification in the Canidæ leads into various difficulties, and he hence purposes a fresh identification. He further points it out as remarkable that the "all-important protocone" is so reduced as to be almost gone in the carnassial tooth, and according to usual identifications, in some other teeth.

Fig. 213 (1).



The accompanying diagrams, which are taken from Flower and Lydekker's "Mammalia," show the modification which the carnassial teeth undergo in various members of the class.

In a general sense we may say that the characters which indicate a pure flesh diet are: the small size of the incisors as compared with the canines, and their arrangement in a straight line across the jaw; the large size, deep implantation, and wide separation from one another of the canines;

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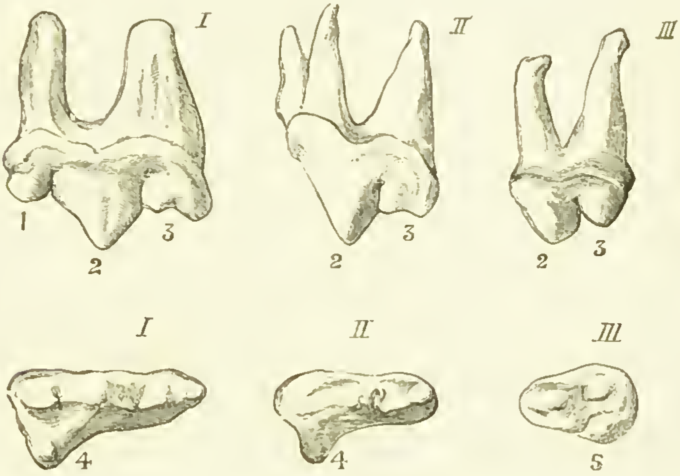
(1) Left lower carnassial teeth of Carnivora. I. Felis. II. Canis. III. Herpestes. IV. Lutra. V. Meles. VI. Ursus. 1. Paraconid. 2. Protoconid. 3. Metaconid. 4. Hypoconid. It will be seen that the relative size of the two roots varies according to the development of the portion of the crown they have respectively to support.

the reduction in number of the molar series, those that remain being without broad crushing surfaces, in the place of which a pointed or sharp-edged form prevails.

Thus the more numerous the teeth of the molar series, and the broader their crowns, the more likely it is that the creature subsists upon a mixed diet; and a gradation may be traced even in individual teeth, such as the carnassials, in which a gradual increase in relative size of the internal tubercular cusps of the upper, and of the posterior tubercles of the lower teeth, may be traced as we pass from the examination of the teeth of Felidæ to those of mixed feeders, such as the Arctoidea.

Fig. 214 (1).



It is a familiar observation that immature animals differ less from their allies than do the respective adults, and this is exemplified by the milk dentition of the present order.

With the exception of the Felidæ, which have only two lower milk molars, the terrestrial Carnivora, so far as is known, all have the same milk dentition:

$$i\frac{3}{3}\ c\frac{1}{1}\ m\frac{3}{3}.$$

---

(1) Left upper carnassial teeth of Carnivora. I. Felis. II. Canis. III. Ursus. 1. Anterior added cusp. 2. Paracone. 3. Metacone. 4. Protocone. 5. Inner posterior cusp, without distinct root characteristic of Ursidæ.

CYNOIDEA.

The Dog presents almost the full typical number of teeth, one upper molar (present in an extinct dog-like animal, the Amphicyon, and sometimes in C. cancrivorus) alone being wanting.

$$i\frac{3}{3}\ c\frac{1}{1}\ pm\frac{4}{4}\ m\frac{2}{3},\quad \text{or}\quad dm\frac{1}{1}\ pm\frac{3}{3}\ m\frac{2}{3}.$$

Thus in Cynoidea the number of teeth varies from forty in Cyon, to forty-six or forty-eight in Otocyon, a fox-like animal.

The incisors are small, the outermost being the largest; the upper incisors have, as in a great many Carnivora, a trilobed shape, the surface of the crown being marked by a transverse groove into which the apex of the lower tooth fits, and the anterior of the lobes thus formed being notched so as to divide it into two.

The canines, large and conical, are somewhat compressed from side to side, and have an anterior and posterior sharp ridge; they are also slightly flattened on their inner surface.

The premolars are flattened from side to side, pointed, increasing in size from before backwards, and have small basal accessory cusps. (See Fig. 215.) The first premolar has no predecessor; it is a small tooth, and is often lost early; it is cut considerably before the other premolars, of which pm4 erupts first; and as its follicle appears about the second week, before there is any trace of the follicle of the other premolar teeth, Lesbre regards it as a persistent milk tooth. From this, however, Marett Tims dissents, regarding it as a permanent tooth. The fourth upper premolar is the sectorial tooth, and is very much larger than the third premolar; the blade is well pronounced, and the tubercle small. The fourth lower premolar does not greatly differ from the third. The two upper true molars are blunt, broad-crowned tuberculated teeth, but the second is very small.

In the lower jaw the first true molar or carnassial tooth has a well-marked blade, which articulates with the blade of the upper carnassial tooth; but towards the posterior border there is a somewhat thick and blunt tuberculate portion, barely represented in the corresponding tooth of the Felidæ; the tubercular portion articulates with the broad flat first upper molar. The second lower molar is smaller, not being one-fourth the size of the first; the third smaller still; both are blunt-crowned tuberculated teeth (the third lower molar, rudimentary in all dogs, is altogether absent in the Canis primævus).

FIG. 215 ([1]).

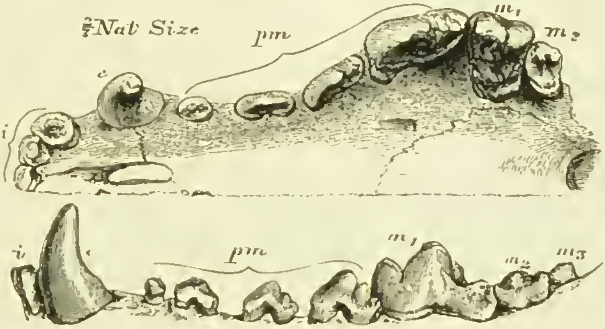
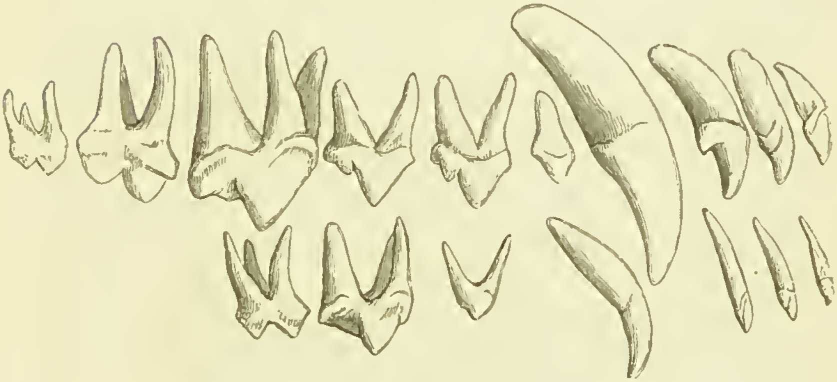


FIG. 216 ([2]).



The dentition of the dog, closely similar as it is to that of the wolves and foxes, is such as to allow of a considerable range of diet, there being tubercular molar teeth in addition to a full armament of such sharply-pointed teeth as are characteristic of flesh-feeding animals.

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[1] Dentition of Australian dog (Canis Dingo).

[2] Milk and permanent teeth of dog. (After Professor Flower.)

Thus the Canidæ, fairly uniform as they are in dentition, have somewhat different habits; the Arctic fox, a flesh-feeder purely, has a dentition indistinguishable from the North Italian fox, which is reputed to be vegetarian in its diet; the Canis cancrivorus of Guiana, which often possesses a fourth molar, eats small mammals, crabs, and also fruit. Hence it is necessary to be very careful in deducing from the character of the teeth what may probably have been the diet of the animal; an approximate idea may often be reached, but the sources of fallacy are sufficiently numerous to render the conclusion uncertain.

Amongst the various breeds of dogs some slight differences exist. Thus, in the long-muzzled races considerable intervals exist between the premolars, as is to some extent seen in C. Dingo (Fig. 215), while in the short-muzzled races, the teeth are in contact, and set somewhat obliquely, so as to overlap irregularly, sometimes the hinder edge of the anterior tooth passing outside and sometimes inside the front of the tooth next behind it.

Otocyon, with its extra teeth, is probably a somewhat primitive form, and it is pointed out by Marett Tims that its teeth are more multicuspidate than those of most of the family.

De Blainville mentions that in long-muzzled dogs supernumerary teeth are met with more often than in short, and on the whole it may be said that the teeth are less easily susceptible of modification in size than are the jaws, so that crowding of the teeth is induced by selective breeding aiming at the production of short-muzzled varieties.

ÆLUROIDEA.

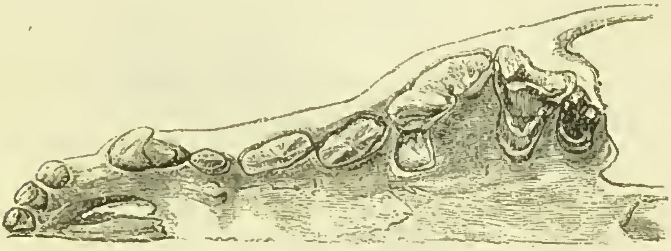
With a dental formula not differing much from the dog (and not at all from Canis primævus) the **Viverridæ** (Civet cats, Ichneumons, &c.) approach the more typical carnivores in such points as the thinner and sharper blades of the premolar teeth and the greater relative length and sharpness of the canines.

The dental formula is—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{2}.$$

At the same time the lower carnassial tooth has no less than six sharply-pointed cusps, and it lacks the typical character of a sectorial tooth, while the long pointed cusps of the molars of some Viverridæ recall the characters of insectivorous dentitions rather than those of true flesh-feeders; furthermore, there are other Viverridæ which are not at all savage, and which subsist on a diet of fruits, eggs, &c., such as the Binturong or the Paradoxurus, the teeth of which have almost lost the carnivorous character. Little use can therefore be made of the Viverridæ as illustrating the transition between the dental characters of the other families of the order; they rather serve to exemplify how, within the limits of a single family, with an identical dental formula, the form and size of the teeth may vary so as to adapt its members to different forms of food and habits of life.

Fig. 217 (¹).



Hyænidæ.—In the **Hyæna** the jaw is short and stout; the canines are set far apart, and the teeth of the molar series are reduced in number.

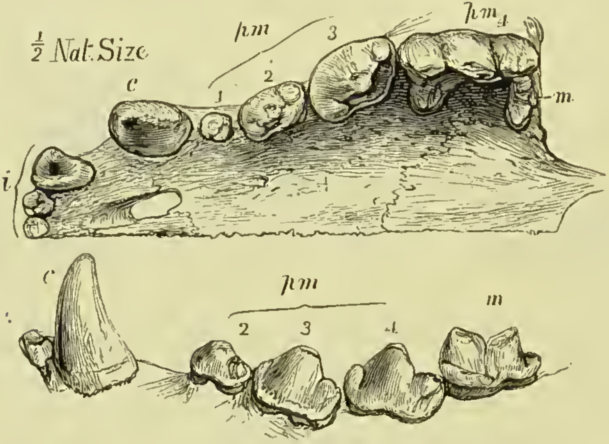
$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{2}{3}\;m\,\frac{1}{1}.$$

(¹) Left upper dentition of Indian civet (Viverra zibettia). (From Flower and Lydekker's "Mammalia.")

The incisors are short and stout, but the outermost upper incisor is somewhat caniniform ; the canines are very strong, but are not so long relatively to the other teeth as in the Felidæ.

The premolars are all stout pointed teeth, with a very well pronounced basal ridge or cingulum, serviceable in protecting the gums when the creature is crushing up bones; they increase in size from before backwards in the upper jaw, the fourth upper premolar being a well-marked carnassial tooth with its blade and tubercle.

FIG. 218 (1).



The lower carnassial or first molar consists of little more than the notched blade ; but the little posterior tubercle so strongly pronounced in the dog, is in the hyæna distinctly more marked than in the Felidæ. (Cf. Figs. 213 and 215.) The only upper true molar is the rudimentary tooth, placed inside the back of the fourth premolar.

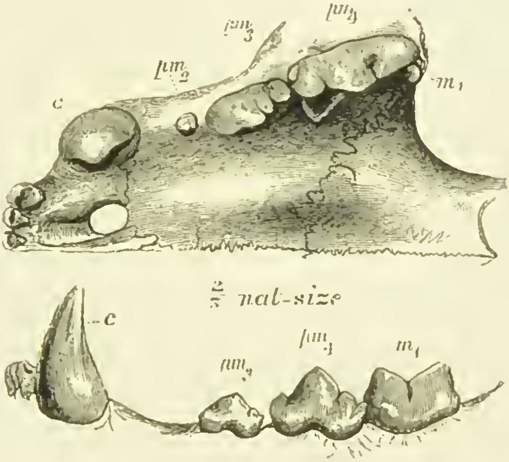
The main feature of the dentition of the hyæna is the great stoutness and strength of the teeth; they are admirably adapted to the habits of the animal, which feeds rather upon the portions of carcases left by the fiercer carnivora than upon those which it kills for itself, and consequently bones form a large proportion of its food.

---

(1) Upper and lower teeth of hyæna. The strongly marked cingulum is seen upon the lower teeth. In the upper jaw the fourth premolar (carnassial tooth) has a strong blade, divided into three cusps, and a small tubercle opposite to and within the anterior cusp ; it is a good typical carnassial tooth.

There is a curious hyæna-like animal found at the Cape (of which there are often specimens at the Zoological Gardens) called Proteles or Aardwolf, in which the teeth of the molar series are quite rudimentary. The incisors (much worn in old animals) and the canines are fairly well developed; the molars and premolars quite stunted.

FIG. 219 (¹).



The deciduous dentition $\left(\text{dm. } \frac{3}{3}\right)$ is similar to the adult, as respects the teeth being stunted. It is a cowardly animal, and is supposed to feed on putrid flesh; it is said to eat young lambs, and to bite the large tails of the Cape sheep, which are remarkable for containing an abundance of semi-fluid fat.

There is also another form, from Madagascar, named Eupleres, which has weak jaws, and a dentition so much reduced that it was at first regarded as an Insectivore.

Felidæ.—The dentition of this family is singularly uniform.

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{2}\;m\,\frac{1}{1}.$$

(¹) Side view of lower, and palatal aspect of upper jaw. (Leopard.)

Thus the molar series is reduced below that of hyæna by the loss of a premolar in both jaws. The incisors are very short, the canines very large, widely apart, and sharply pointed, with a pronounced longitudinal ridge very characteristic of the Felidæ; the premolars nearest to them are quite short, so that they stand practically alone, and so can penetrate the flesh of living prey more readily.

The first upper (really the second of the typical mammalian dentition) premolar is almost a rudimentary tooth; the second, a far larger tooth, is sharply pointed; the last is a well pronounced carnassial tooth, of which the "blade" is divided by two notches into three sharp lobes, with the middle one of which the "tubercle" is connected by a slight ridge.

The solitary true molar is a small tooth, placed transversely, and within the back of the premolar, so that looking from the outside it is not visible at all.

In the lower jaw the carnassial (first molar) is reduced to the "blade" only; it is divided by a V-shaped notch into two lobes, and the posterior tubercle is hardly represented.

In an extinct feline animal, the **Machairodus**, found in tertiary strata, and very widely distributed (in France, Italy, India, Brazil, Buenos Ayres), the first of the premolars left in the upper jaw of Felis, and there almost rudimentary (see Fig. 219), has disappeared; the dental formula is thus:

$$\text{i}\,\frac{3}{3}\,\text{c}\,\frac{1}{1}\,\text{p}\,\frac{2}{2}\,\text{m}\,\frac{1}{1}.$$

The upper canines are of immense length, and the ridge of enamel which runs down the front and back surface of the teeth is distinctly serrated; hence the name of saw-toothed Tiger which has been given to the animal.

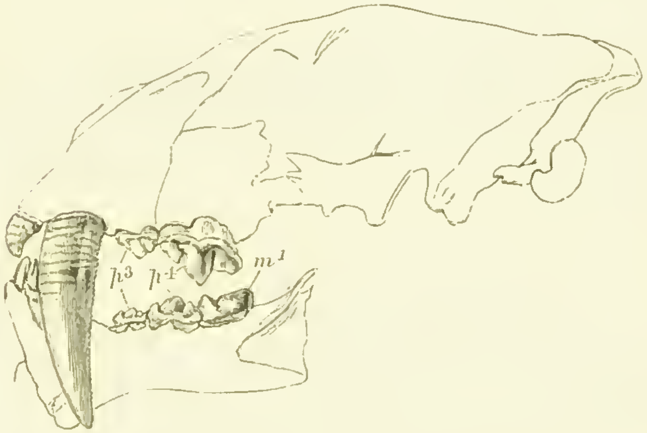
The lower canines are quite small, and range with the incisors. The enormous length of the upper canine renders it difficult to see in what manner it was made use of, as the mouth could hardly have been opened to an extent sufficient to enable its point to do more than clear the lower jaw.

Smilodon, a somewhat similar extinct animal, had a dentition still further reduced, viz. :

$$i\,\frac{3}{2}\;c\,\frac{1}{1}\;p\,\frac{2}{2\text{ or }1}\;m\,\frac{0}{1}.$$

Professor Cope has described a rich series of extinct cats ("Extinct Cats of N. America," "American Naturalist," Dec. 1880), mostly from Miocene beds. He summarises their characters thus :

FIG. 229 (¹).



"It is readily perceived that the genera above enumerated form an unusually simple series, representing stages in the following modification of parts :—

(1.) In the reduced number of molar teeth.
(2.) In the enlarged size of the upper canine teeth.
(3.) In the diminished size of inferior canine teeth.
(4.) In the conic form of the incisors.
(5.) In the addition of a cutting lobe to the anterior base of the upper sectorial tooth.
(6.) In the obliteration of the inner tubercle of the lower sectorial.
(7.) In the extinction of the heel of the same.

(¹) Side view of the jaws and cranium of Machairodus (Drepanodon). (After Owen.)

(8.) In the development of an inferior flange at the latero-anterior angle of the front of the ramus of the lower jaw.

(9.) In the development of cutting lobes upon the posterior border of the large premolar teeth.

The succession of the genera above pointed out coincides with the order of geologic time very nearly.

The relations of these genera are very close, as they differ in many cases by the addition or subtraction of a single tooth from each dental series.

These characters are not even always constant in the same species, so that the evidence of descent, so far as the genera are concerned, is conclusive. No fuller genealogical series exists than that which I have discovered amongst the extinct cats."

ARCTOIDEA.

Amongst the Carnivora grouped together by many characteristics as "bear-like," a tolerably complete gradation of character in the matter of dentition may be traced.

Some of the group, such as the stoats and martins, are very carnivorous; others are mainly herbivorous. Of the **Mustelidæ** the dental formula is—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{1}{2}.$$

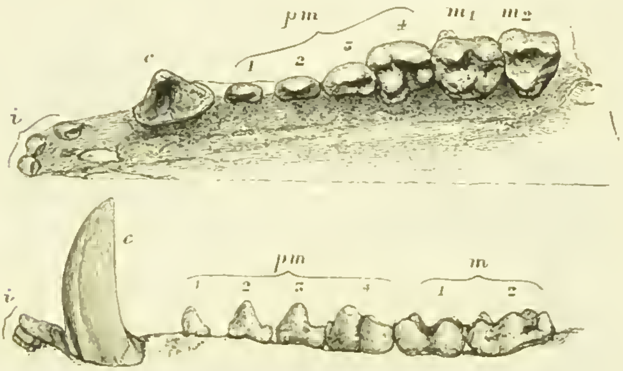
There is a sort of *primâ facie* resemblance to the feline dentition, for the sectorials are very much like those of the Felidæ, but the last tooth in each jaw is a broad-topped tubercular molar, even in the most carnivorous members of the group, while in those which are less so, such as the badger, the molar teeth are very broad and obtuse, the lower sectorial having a very small blade and a very large tubercular posterior talon, so that, without having really lost its typical formation, it comes practically to be a broad grinding tooth.

In the **Procyonidæ** (Racoons and Coatimundis, &c.), we have a further departure from the carnivorous character, in the increased development of the molar series: the dental formula is —

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{2}.$$

In the **Coatimundi,** for example, the upper sectorial has a very large “tubercle,” and posteriorly to this there is a small additional tubercle; the “blade has no large or conspicuous thin, flat, sharp edge, but presents two pronounced cusps.

Fig. 221 (1).



The lower sectorial is no longer recognisable as a carnassial tooth, and all the true molars are broad teeth with four or five cusps.

The canines are very peculiar, those of the upper jaw being very straight and much flattened from side to side; those of the lower jaw strongly curved, and marked by a deep groove near the front of their anterior surface.

The first premolar is in many of the Mustelidæ rudimentary, and is lost early, but there is not enough known of it to enable us to decide whether it is a persistent milk tooth, or a deciduous second tooth.

---

(1) Upper and lower teeth of a Coatimundi (Nasua socialis). The fourth upper premolar (carnassial tooth) has lost its sectorial character by the blade being much less, and the tubercle much more developed than in the Æluroidea; there is an additional internal tubercle at the back of the tooth.

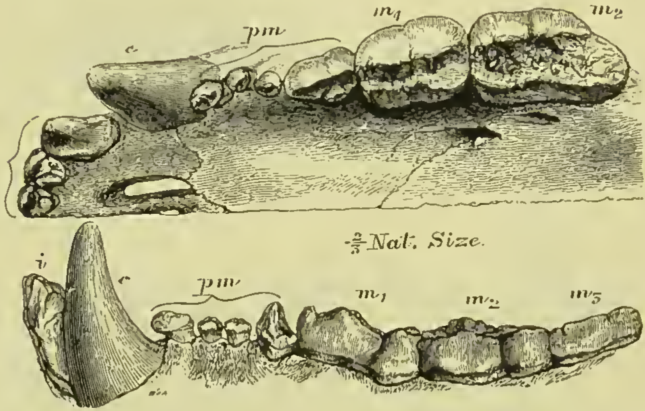
In the **Bears** the teeth are yet further modified to suit the requirements of mixed or vegetable feeders.

The dental formula is generally—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{2}{3}.$$

The incisors of the upper jaw present the notch across the crown, so common in Carnivora, and the outermost is large and not unlike a canine; the canines are, relatively to the other teeth, not so large as in dogs or Felidæ; nevertheless they are stout, strong teeth, upon which the anterior and posterior ridges of enamel are well marked.

FIG. 222 ([1]).



The first three premolars are small, dwarfed teeth; the first premolar is very close to the canine, and has a crown of peculiar form, produced out towards the canine.

All four of the premolars seldom persist through the lifetime of the animal; the first premolar, however, is rarely (if ever in recent species) lost, the second being the first to fall out, and then the third. As the fourth is never lost, in most adult bears the first and fourth premolars are found with a wide interval between them. The premolars of bears thus form an exception to the rule that when

[1] Teeth of a bear (Ursus thibetanus ?). The figure is drawn from a young specimen, in which the canines have hardly attained to their full length. In this bear the four premolars are all persistent.

a tooth is lost from the premolars, the loss takes place from the front of the series.

The fourth upper premolar (carnassial tooth) retains something of its carnassial character, though relatively to other teeth it is smaller than in the Felidæ; the first lower molar very little, save that it is a narrower and more elongated tooth than the other true molars.

The other true molars are squarish or oblong teeth, raised into blunt tubercular cusps; they vary in different species.

In the sloth bear (Melursus labiatus) the incisors are small and the median pair are lost early; it is variously stated to be frugivorous and to feed on ants, the latter probably being the more truthful account.

CARNIVORA PINNIPEDIA (SEALS).

The aquatic Carnivora are divided into three families :—

I. The Otariidæ, or Eared Seals, comprising the single genus Otaria, known as Sea Lions, or Sea Bears. These are the "fur seals," from which sealskin is procured, and they are less removed from the terrestrial carnivora than are the other seals : the limbs are better adapted for walking, there are external ears, &c.

II. The Phocidæ, to which family the seals of our own coasts (Phoca greenlandica, &c.) and the Great Proboscis Seals of the southern seas (Cystophora) belong.

III. The Trichechidæ, or Walruses, an aberrant Arctic family consisting of one genus only.

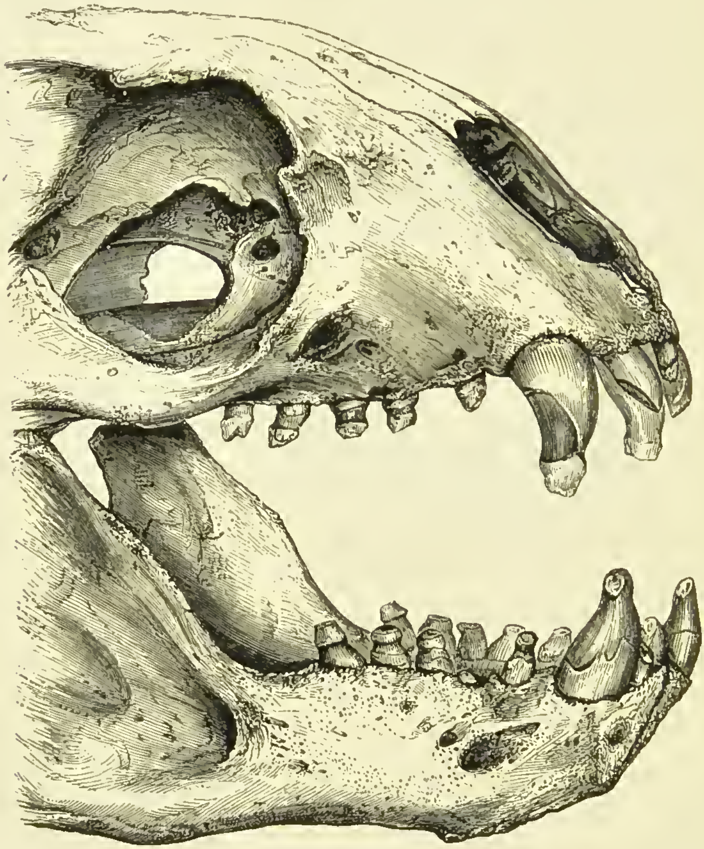
The dentition of the **Seals** is less highly specialised than that of other Carnivora, in some cases approximating to that of homodont Cetaceans.

The seals belong to the less powerfully developed orders of mammalia, and like others similar in this respect, have no change of functional teeth.

What change there is takes place at an exceedingly early period, indeed at or before birth.

The milk dentition is very feebly developed in all seals; in the Otaria (fur seal) which of all the seals most approaches to the terrestrial carnivora in other characters, the milk teeth are retained for a few weeks, but in most others they are shed about the time of birth. Thus Professor Flower tells us that in a Phoca greenlandica a week old scarcely a trace of the milk teeth was left.

FIG. 223 (1).



The canines are generally well marked by being larger than the other teeth, but the molars and premolars are very similar to each other, and are simple in pattern.

The teeth of **Otaria** and of some other seals become much worn down, and they also seem to become eroded at the level of the gums, as they are often deeply excavated at points which seem unlikely to have been exposed to friction, but the nature of this erosion has not been adequately investigated.

---

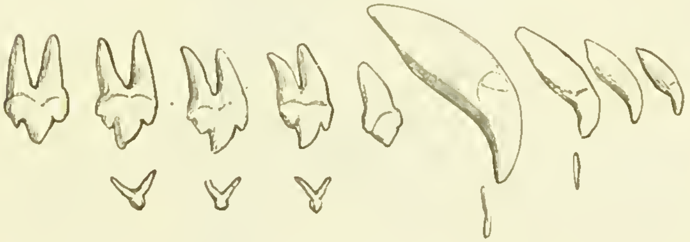
(1) Jaws of Otaria, in which the teeth are affected by a form of erosion. (After Dr. Murie.) "Odont. Soc. Trans.," 1870.

Otaria has a dental formula—

$$i\,\frac{3}{2}\;c\,\frac{1}{1}\;pm\,\frac{4}{4}\;m\,\frac{1\text{ or }2}{1}.$$

The first premolar has no predecessor either in it or in the Phocidæ.

Fig. 224 (1).



The incisors, however, vary in number in different groups, while the canines, premolars, and molars are constant.

The common seals (**Phoca**) have a dental formula—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{1}{1}.$$

The incisors are of simple form, and the outer are the larger. The canine is a strong recurved tooth, with a large root; behind it follows a series of molars, each of which (with the exception of the first) bears a central principal cusp, with a smaller accessory cusp before and behind it. The forms of the crowns vary a good deal in different genera, in some the cusps being much larger, more deeply separated from one another and recurved; and in others the accessory cusps being multiplied, so that the name of "saw-toothed seal" has been given to their possessor.

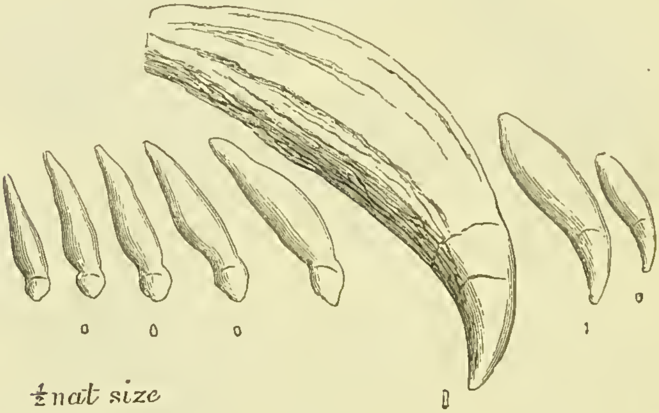
(1) Teeth of Phoca greenlandica.

It is suggested by Baume that the degree to which the teeth have become simplified perhaps corresponds with the antiquity of the genus as aquatic, those which have taken to the water more recently having retained a greater complexity of tooth crown.

The Leopard Seal has teeth with exceedingly long roots, disproportionate, one would say, to the necessities of a fish feeder for firmness in the implantation of its teeth.

In the Hooded Seals (Cystophora) the incisors are reduced to one in the lower jaw and two in the upper; the canines are of great size, but the molars are small and simple in form, so as to approximate to the teeth of the Cetacea.

FIG. 225 (1).



But it is noteworthy that whereas the Cetacea arrived at a monophyodont and homodont dentition by the suppression of the second dentition, and retain their milk teeth, the converse is true of the seals.

The Walrus (Trichechus rosmarus), an aberrant Arctic form, is possessed of enormous upper canines, which pass down outside the lower lip, and are of such dimensions as to materially modify the form of cranium by the size of their sockets; they grow from persistent pulps, and are composed of dentine with a thin investment of cement.

The great tusks are employed to tear up marine plants and to turn over obstacles, the walrus feeding upon crustacea, and also upon seaweed, &c.; they are also used to assist the animal in clambering over ice: as they are of almost equal size in the female, they cannot be regarded as weapons of sexual offence, but they are undoubtedly used in the combats of the males.

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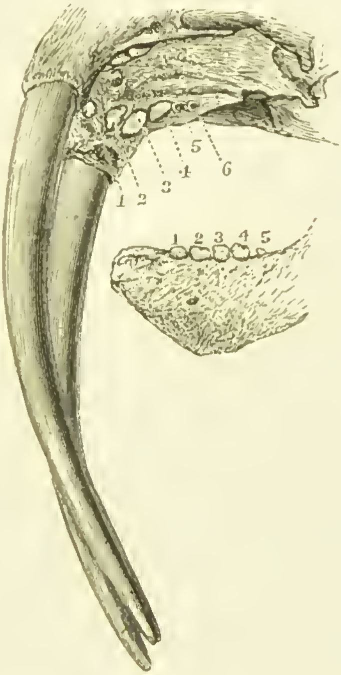
(1) Permanent and milk teeth of elephant seal (Cystophora proboscidea).

FIG. 226 (1).



The largest tusks seen by Nordenskiold were 30 inches in length, and 8 inches in circumference; the tusks of the females attain to the same length, but they are much more slender.

In addition to the great tusks the walrus ordinarily has a row of four or five teeth, short and simple and worn down to the level of the gums. Of these, the one placed immediately within the base of the great canine is in the intermaxillary bone, and is hence an incisor: the ordinary dental formula is given by Professor Flower as—

---

(1) Side view of upper and lower jaws of a walrus (Trichechus rosmarus). The upper jaw has been tilted a little to one side, in order to bring into view the molar teeth at the same time with the long tusks. The determination of the teeth being open to question, they have been simply numbered.

$$i\,\frac{1}{0}\;c\,\frac{1}{1}\;p\,\frac{3}{3}.$$

But there is some difficulty in assigning a definite dental formula: for in front of the solitary incisor are often the sockets (or even the teeth themselves) of two others, which are for various reasons rather to be regarded as non-persistent teeth of the permanent set than as milk teeth: and there are small teeth sometimes to be met with behind the molars, which also seem to be rudimentary permanent teeth.

In young specimens the dentition is—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;\text{pm and m}\,\frac{5}{4}.$$

The teeth above alluded to may persist through life, and probably often do; but they are sure to be lost in macerated skulls, as they have but little socket. Of the milk dentition four teeth have been traced in each jaw; they are rudimentary, are lost about the time of birth, and correspond in position to the more largely developed teeth of the adult. Hence the question if those small rudimentary teeth above alluded to are to be regarded also as milk teeth, which are long retained, or as rudimentary permanent teeth; at present this requires further elucidation.

CHAPTER XIII.

THE TEETH OF INSECTIVORA AND CHIROPTERA.

THE Insectivora form rather a heterogeneous order of Mammals, and embrace very various forms. All of them are of rather small size, and some are very small indeed. Their diet consists for the most part of insects, and their teeth are generally adapted for this by being furnished with many points. The best known animals in the order are the Hedgehogs, the Shrews, the Moles, and the Macroscelidæ (Elephant mice); to these is to be added the Galeopithecus, or "Flying Lemur." Insectivora are more abundant in Africa, Asia, and South America than in Europe. The Shrews approximate in some measure towards the Rodents, and the Tupaia is very lemurine in its characters.

They all have small brains and long faces. The Insectivora are ancient and in some respects rather generalised mammals, so that they may be supposed not to have diverged so far from the parent forms as other mammalia. Professor Cope has described a good many genera which have been found in American Eocene Strata, and some of these, *e.g.*, **Mesonyx**, had teeth differentiated into incisors, large canines, premolars and molars.

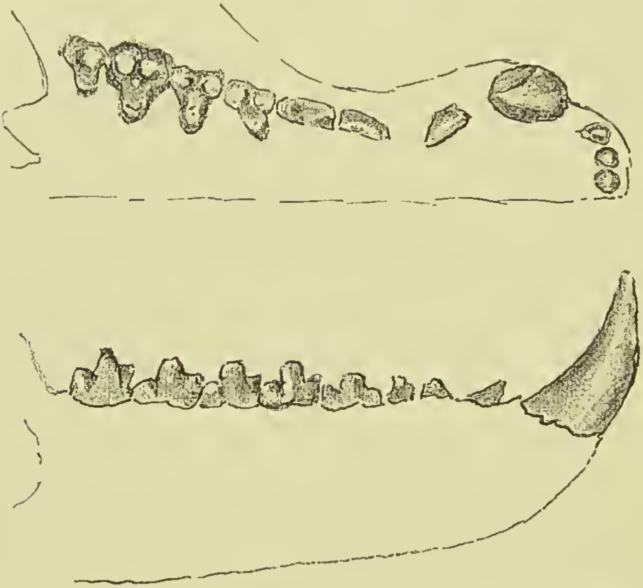
The incisors were small and their crowns more or less conical. The upper canines were large, strongly recurved, and sharply pointed, with a considerable diastema in front of them; the first premolar was single-rooted but the other three had two roots; their crowns were compressed, having a principal cusp and a posterior lobe with a cingulum; the fourth was a little more complex than the others, and was more typically trituberculur.

The upper molars were tritubercular, with a strongly pronounced cingulum at the back, the last molar, however, lacking the postero-external cusp.

The lower premolars and molars are rather simple; the first is single-rooted and conical, the others having two roots and a principal cusp, to which are added small anterior and posterior cusps, elevations of the cingulum.

From such a dentition, as Dr. Wortman points out, more complex patterns can easily be derived by additions to the front and back of the cones and by the elevation of a cingulum, from which additional cusps can be formed.

Fig. 227 ([1]).



Its dental formula was—

$$i\,\frac{3}{2}\,c\,\frac{1}{1}\,pm\,\frac{4}{4}\,m\,\frac{3}{3}.$$

Of the teeth of early Insectivora it may be said that it would not be difficult to imagine how the teeth of all other Diphyodont Mammals might be evolved from them,

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([1]) Upper and lower dentition of Mesonyx ossifragus. (After Cope.) One-third nat. size.

whilst Professor Cope ("Proc. Acad. Nat. Sc. Philadelphia," 1883, and *passim ;* see also Dr. Wortman, "Americ. System Dental Surgery," Teeth of Vertebrata), gives an admirable series of extinct genera in which the molar patterns become more complex, and approximate on the one hand to the sectorial teeth of Carnivora, and on the other to the bristling cusps of modern Insectivora.

In recent Insectivora the canines are often not sharply differentiated from the incisors, and sometimes a tooth clearly of the premolar group is differentiated to serve as a canine, but as this does not occur in the earlier Insectivora it is evidently a feature acquired subsequently.

It hence happens that different writers give different dental formulæ to the Insectivora, the differences mainly turning upon whether any tooth is called a canine or not. (Cf. p. 348.) But, as pointed out by Leche and Marsh, in the oldest known mammals this tooth was always two-rooted, and the reduction to one root goes on somewhat, but not absolutely, with the caniniform specialisation of its crown. Hence, when it has but one root this is a character acquired, and not an original distinction.

In Insectivora the extent to which a milk dentition is developed varies much ; thus in many of the group it is cut and lost early, and is more or less suppressed ; whilst in others, *e.g.*, Centetes, Hemicentetes, Macroscelides, and Tupaia, it is well-developed and is functional for some time, whilst in Galeopithecus all the permanent molars, with but a slight exception, range with and work with a full milk dentition.

Galeopithecus stands alone : it was formerly, and is indeed sometimes even now, placed with the Lemurs ; but it has much more in common with Insectivora. The teeth are somewhat anomalous, the lower incisors being divided by a number of vertical divisions running down through a great part of the length of the crowns, so that they can be compared to combs, or to hands with the fingers slightly separated. What the purpose served by these comb-like teeth may be remains uncertain : no other animal has similar teeth.

It has been supposed that these teeth are used by the animal in combing its fur, but Leche ridicules this interpretation, deeming it far more probable that they have relation to peculiarities of food. Unlike most Insectivora, Galeopithecus feeds on fruits and leaves. The so-called canine, which Leche prefers to call the first premolar, is two-rooted, as happens in many Insectivora, but Galeopithecus stands almost alone among recent mammals in having $\underline{i_2}$ two-rooted; Leche points out that this is no real distinction from Insectivora, as Petrodromus has it two-rooted, whilst in the genus Erinaceus it may be found in different species sometimes distinctly two-rooted, sometimes one-rooted.

For Galeopithecus Leche ("Svenska Vetenskaps Akad.," Bd. XXI. No. 11, 1886) gives the following dental formula—

$$i\,\frac{2}{3}\ pm\,\frac{3}{3}\ m\,\frac{3}{3}.$$

Galeopithecus has a milk dentition more complete than most Insectivora; the milk dentition is developed late, no teeth being cut in a fœtus just born, and in one which had a full coat of hair only the points of $\underline{dm_3}$ and $\overline{di_1\ di_2\ dm_3}$ were through the gums. At this time no successional teeth were far advanced, but all the true molars were as far advanced in calcification as the milk teeth, and lay but little deeper in the jaws.

Hence it comes about that in Galeopithecus all the molars (except $\underline{m_3}$) are up in place and at work during the persistence of all the milk teeth. This appears to be an argument in favour of regarding the true molars as homologous with the milk teeth.

There is this further peculiarity, that the so-called di_3, described by Owen, is really $\overline{pi_3}$, which is in place, and at work with, the milk teeth for a considerable time, di_3 being a small tooth lost early. The back teeth, both of first (dm) and of second dentitions (pm), present gradated stages of differentiation from the molar type; thus dm_2, contrary to the general rule, differs more widely from the molar type than does its successor; dm_3 and pm_3 are quite alike.

From these peculiarities Leche concludes that the dentition of Galeopithecus is an ancient inheritance, and that for a very long time it has been fully adapted to its manner of life.

The common **Hedgehog (Erinaceus)** has the following dental formula—

$$i\,\frac{1\ 2\ 3}{0\ 2\ 3}\ e\,\frac{1}{1}\ p\,\frac{0\ 2\ 3\ 4}{0\ 2\ 0\ 4}\left(\text{or } p\,\frac{1\ 2\ 0\ 4}{1\ 0\ 0\ 4}\right)m\,\frac{1\ 2\ 3}{1\ 2\ 3}\ \text{(Woodward).}$$

Leche, after an examination of 103 specimens belonging to seventeen species, gives us a formula common to the genus—

$$i\,\frac{1.2.3}{0.2.3}\ e\,\frac{1}{1}\ p\,\frac{2\ 3\ 4}{0\ 3\ 4}\ m\,\frac{1.2.3}{1.2.3}.$$

But a good many dental formulæ have been assigned to it, as there are certain difficulties and obscurities in the identification of its teeth, which have only lately been cleared up.

The differences arise chiefly because the canines are not very caniniform; they are implanted by two roots, and they appear to be some little way behind the intermaxillary suture.

But it has been found that they were preceded by single-rooted caniniform teeth, and that the distance from the suture is apparent and not real, as it is due to the maxilla growing forward and embracing the premaxilla both on its labial and palatine aspects. In a young specimen in my possession, prior to this overlapping of the maxilla the canine is seen to be close to the suture.

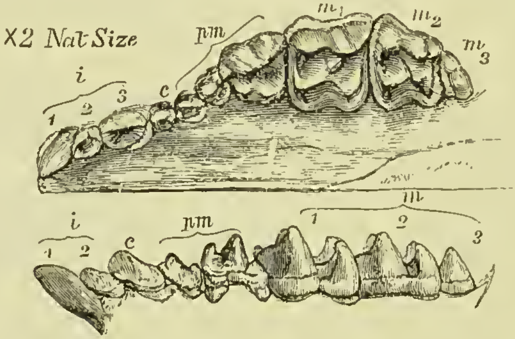
In the upper jaw there is a rather wide interval between the first pair of incisors, which are much the largest, lean inwards towards one another, and are somewhat caniniform in shape. The second pair of incisors are much smaller, whilst the third are larger and caniniform, though they do not equal the first in length. The canine, though it has an indication of division into two roots, is not a very large nor important tooth.

Leche ("Anat. Anzeig.," 1897) figures this tooth from four specimens of E. europæus, showing that it varies in the same species between a tooth in all respects like a premolar and a powerful, though still two-rooted, canine. It is followed by two small single-rooted premolars, of which the second is variable and sometimes absent, and then by a large (fourth) upper premolar.

The fourth upper premolar is totally different in size and form from the third: its crown is large, squarish, and furnished with four cusps, of which the antero-external one is far the longest and sharpest.

The first upper true molar has a square crown, upon which are four sharp cusps, and in an unworn tooth a fifth small central cusp, and it is implanted by four roots. The second true molar is also square, quadricuspid, and has four roots; but it is much smaller than the first, while the third upper true molar is quite a small, compressed, double-rooted tooth, with a thin-edged crown.

Fig. 228 (1).



In the lower jaw the first incisors, really the second of the typical mammalian dentition, less widely separated than the upper, are also the largest; then follows another tooth termed incisor, on account of its relation to the upper incisors when the mouth is closed. The third tooth is much larger, and of peculiar form, and is the canine according to recent writers. The fourth tooth from the front is a small single tooth, like the third, but upon a smaller

(1) Upper and lower teeth of the hedgehog.

scale. Next behind it comes a tooth which is very much larger, and its crown carries two principal cusps with a small subsidiary cusp ; this is certainly a true premolar. The next tooth (first true molar) has an oblong crown beset with five sharp cusps, of which four are arranged at the corners of a square, while the fifth, perhaps an elevation of the cingulum, lies a little in front and towards the inside of the tooth. In the second true molar the fifth cusp is but little indicated, while the last true molar is a dwarfed tooth with but one cusp.

The teeth of the Hedgehog fairly represent some of the features of Insectivorous dentitions, for the forcep-like incisors, the stunted or non-developed canines, and the molars bristling with pointed cusps, are common to very many of the order.

In the upper quinquecuspidate molars, the two outer cusps are the paracone and metacone, the two inner the protocone and hypocone, and there is a small central metaconule. Of these the order of development was—

Paracone
Metacone } Trigon.
Protocone
Hypocone.
Metaconule.

In the lower molars the five cusps are those of the Trigon with two extra cusps, the internal entoconid and external hypoconid. Owing to the partial suppression of the paraconid, and the protoconid and metaconid being joined by a ridge, as are the entoconid and hypoconid, the resultant tooth is squarish with two transverse ridges. The order of appearance of the cusps is—

Protoconid.
Metaconid.
Entoconid.
Hypoconid.
Paraconid.

Thus in their order of appearance, in neither upper nor lower teeth, do the cusps fit in with what might have been expected on the tritubercular theory.

In the last edition of this book the persistent dentition of the Hedgehog was stated to be a mixture of replacing teeth with persistent milk teeth. This view, which was given on the authority of Leche, has been proved by that observer (3) and by Woodward (2) to be incorrect, and it has been found that all of the teeth which persist have been preceded by tooth vestiges in various degrees of reduction.

Some of the milk teeth are well developed and functional; others, notably the upper canine, very variable in the extent to which they are developed, whilst others again are functionless and never cut the gum, but are represented by tooth germs which undergo development only to the extent of a trifling irregular calcification.

The formula of the milk dentition may be written thus, the teeth which are functionless being printed in italics—

$$\mathrm{i}\,\frac{1\;2\;\mathit{3}}{\mathit{1}\;2\;\mathit{3}}\,\mathrm{c}\,\frac{1}{\mathit{1}}\,\mathrm{p}\,\frac{\mathit{0}\;\mathit{2}\;3\;4}{\mathit{0}\;\mathit{2}\;\mathit{3}\;4}\left(\mathrm{or\ p}\,\frac{\mathit{1}\;2\;\mathit{3}\;4}{\mathit{1}\;\mathit{0}\;\mathit{3}\;4}\right)$$

The deciduous upper canine has been found to vary between being a minute irregular calcification (Woodward, Leche) and being a functional tooth. (Cf. Fig. 166.)

In the molar region there are to be found both a lingual continuation of the dental lamina and a slight, but constant, outgrowth on the labial side of the neck of the enamel organ of the functional tooth (Woodward [1]), not distinguishable from those incisor germs which calcify a little. He therefore concludes that there are evidences of a vestigial set, of a functional set, and of a lamina capable of going on to form an additional set in the molar region.

The Gymnura, an animal of the Malay region, closely allied to the Hedgehog, but in appearance more like a very big Shrew, with a body a foot long, is somewhat peculiar in possessing the whole typical number of teeth, its dental formula being

$$\mathrm{i}\,\frac{1\;2\;3}{1\;2\;3}\,\mathrm{c}\,\frac{1}{1}\,\mathrm{p}\,\frac{1?\;2\;3\;4}{1?\;2\;3\;4}\,\mathrm{m}\,\frac{1\;2\;3}{1\;2\;3}.$$

The teeth somewhat nearly resemble those of the Hedgehog, as in it the upper canine is two-rooted, though preceded by a single-rooted deciduous tooth. Knowledge of its milk dentition is owing to Thomas [2] and to Woodward.

$$\mathrm{di}\,\frac{1\;2\;\mathit{3}}{1\;2\;3}\,\mathrm{dc}\,\frac{1}{1}\,\mathrm{dpm}\,\frac{1\;\mathit{2}\;3\;4}{1\;\mathit{2}\;3\;4}.$$

Thus, although it has four premolars retained in its functional dentition, there is a doubt whether p $\frac{1}{1}$ are not retained milk teeth. As in so many other mammals, no vertical replacement of this tooth is known, and, according to Woodward, the relation of the tooth germ of this tooth to the dental lamina is such as to suggest its being a milk tooth, with the lamina continued beyond it so as to have a potential source for a successor. Woodward, however, remarks that there may possibly be a later development of a

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(1) On the Teeth of Certain Insectivora, "Proc. Zool. Soc.," 1896.
(2) "Proc. Zool. Soc.," 1892.

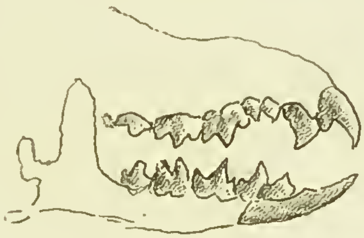
successor, as the p $\frac{1}{1}$ of the adult seems rather a stouter tooth than that of the young animal.

The second milk premolars are vestigial, and their successors prematurely developed; the third and fourth premolars are strongly developed. There is thus a pretty complete functional milk dentition, viz., $\frac{di_3}{}$ and $\frac{dpm_2}{dpm_2}$ only being vestigial.

Centetes has typical canines like a Carnivore. Hemicentetes has canines which in no respect differ from those premolars behind it, and Ericulus has a sharp, long, two-rooted upper canine in pattern of crown, an enlarged edition of the premolars behind it. There is no caniniform tooth in the lower jaw.

The **Shrews** have numerous sharply-pointed teeth, the points interdigitating and fitting very closely together when the mouth is shut. There is no tooth either in the upper or lower jaw which is so elongated as to deserve the name of canine; but between the incisors and the true molars are several small teeth which, by analogy, are called premolars. The true molars are not very different in pattern from those of the mole (B in Fig. 231), and present the W-contour so common in the molars of Insectivora.

Fig. 229 (¹).



The most marked peculiarity in the dentition of the Shrews lies in the form of their incisors. The first upper incisor is always very large indeed; it looks vertically downwards, is a little hooked, and has a notch, and a second low cusp behind the principal long pointed cusp. The tip of the lower incisor fits into this notch. The lower incisor is also very large; it lies nearly horizontally, though the point is

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(¹) Teeth of the common shrew, × 3.

bent a little upwards. Along its upper edge there are, in most species, three or four small cusps, while its lower border is curiously prolonged outside the bone of the jaw, so as to in some measure encase this latter. The lower incisor is at least one-third as long as the whole alveolar border. The incisor teeth of the Shrew would appear to form a very efficient pair of pincers, with which to pick up the minute creatures on which it feeds.

It is difficult to assign a dental formula to the Shrews, as the premaxillary suture is lost early and there is no differentiated canine. Brandt considers that there are four upper incisors, because the fourth upper tooth appears to be in the premaxilla; but, as Woodward points out, in all Insectivora the relation of the canine to the intermaxillary suture is more variable than in other orders, and moreover the gap between the maxilla and premaxilla is so large in a fœtus (1·2 inches long) that there were several tooth germs in the gap. On the whole its probable dental formula is

$$i\,\frac{3}{2}\;c\,\frac{1}{0}\;p\,\frac{3}{1}\;m\,\frac{3}{3},$$

though the upper canine is abnormally situated, and Dobson (5) does not allow the existence of a canine at all. A great deal of doubt has rested upon its milk dentition, some authors claiming that calcified milk teeth existed, and others (Leche) denying the existence of any milk dentition in any stage of suppression.

Woodward, however, examining a fœtus a trifle smaller than Leche's, describes and figures well differentiated milk tooth germs to many of the teeth. None of them, however, apparently undergo any calcification, though proceeding so far as the formation of the bell-shaped enamel organs. All of the incisors, canines and premolars show traces of these milk tooth germs, though some are less differentiated than others. The great first incisors show an anomalous condition, namely, a large but not highly differentiated outgrowth on the wrong or lingual side of the functional tooth germ;

yet it can hardly be supposed that these great and peculiar teeth are persistent milk teeth.

There is thus a highly-reduced milk dentition, none of the germs being known to calcify.

$$\text{di}\ \frac{2\ 3}{}\ \text{dc}\ \frac{1}{}\ \text{dpm}\ \frac{3.4}{4}.$$

The dentition of the **Mole (Talpa)** has been the subject of much controversy, the determination of its canines, &c., presenting such difficulty that no less than five different dental formulæ have been assigned to it.

In the front of the upper jaw come three small teeth, the first being somewhat the largest, which are well within the limits of the intermaxillary bone, and are doubtless incisors. But the next tooth, which is very big, also appears to be implanted in the premaxilla, the suture passing across its socket close to the back of its posterior root. The difficulty in accepting this tooth as the true canine was formerly considerable, but is now diminished by the established fact that the relations of this tooth to the suture are variable in Insectivora, and that the two-rooted tooth of Gymnura is without doubt the canine. The mole has forty-four teeth, and the dental formula usually assigned to it is—

$$\text{i}\ \frac{1\ 2\ 3}{1\ 2\ 3}\ \text{c}\ \frac{1}{1}\ \text{p}\ \frac{(1)\ 2\ 3\ 4}{(1)\ 2.3.4}\ \text{m}\ \frac{1\ 2\ 3}{1\ 2\ 3}.$$

Woodward, however, gives reasons for the belief that $\text{p}\ \frac{1}{1}$ is a persistent milk tooth, in which case its premolar formula should be written thus—

$$\text{p}\ \frac{\text{dpm}_1\ 2\ 3\ 4}{\text{dpm}_1\ 2\ 3\ 4}.$$

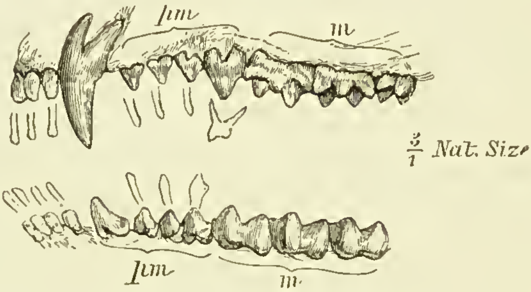
Next behind the canines come three small premolars, and a fourth which is much larger than the others: the three have somewhat simple crowns consisting of single sharply-pointed cusps, whilst the fourth is more molariform.

The first two upper molars are large teeth, bristling with cusps; the third is much reduced in size and simplified in pattern. Woodward calls them of tritubercular or tuberculo-sectorial order. (See Fig. 231.)

The lower molars have a large heel, so large as to preponderate over the Trigon. In the lower jaw the *four* front teeth are all small, but the fourth or outermost of these incisors is called by some writers the lower canine, because, when the teeth are closed, it passes in front of the upper caniniform tooth.

Nevertheless the tooth which does the work of a canine in the lower jaw is the fifth counting from the front: this is a two-rooted tooth, and conforms so closely with the three teeth behind it in configuration, that it is obviously only one of these premolars developed to a greater length than the others. It closes *behind* the caniniform upper tooth, so cannot on this ground be called a canine by those who attach homological importance to the term.

Fig. 230 (¹).



The remaining three premolars are rather small and single rooted; the true molars are of considerable size, and their points are very long and sharp.

The late Mr. Spence Bate's paper ("Trans. Odontol. Society," 1867), valuable as it is in contributing to our whole knowledge of the milk dentition of the creature, does not finally determine the homologies of the canine.

In a Mole 3¾ inches long he found eight milk teeth on

(¹) Upper and lower teeth of the common mole. The functionless milk teeth (after Spence Bate) are placed above the permanent teeth which displace them, with the exception of the deciduous canine, which is placed too far back, over the first premolar.

each side of both upper and lower jaws. The milk incisors were about one-twentieth of an inch in length, and one two-hundredth in diameter, and were rudimentary in form, consisting of long thin cylindrical tubes surmounted by slightly expanded crowns. All the milk teeth were of this simple form, save only the last in each jaw, which presented crowns with two cusps, and had their roots to some little extent divided into two.

At the time when these teeth are present the intermaxillary suture is very distinct, and he had no doubt that the fourth upper milk tooth, the predecessor of the canine, was in the premaxilla.

None of the teeth had fairly cut the gums, and the advanced state of the permanent teeth beside them made it doubtful if they ever did become erupted.

The subject has been re-investigated by Woodward, who confirms in most respects the accuracy of Spence Bate's account. But in one point he disagrees: he was unable to find (in clarified jaws as well as in serial sections) any trace of the deciduous predecessor figured by Spence Bate over the $\text{pm}\,\frac{1}{1}$: on the contrary, he found that $\frac{\text{dpm}_1}{\text{dpm}_1}$ was larger than the other milk teeth, was uncalcified and more backward in development, but occupied a position corresponding to the reduced milk series. Moreover, there was a lingual bud from the dental lamina, indicating that the tooth germ under observation was really the milk tooth. He therefore concludes, after an examination of eight specimens, that there is no permanent tooth developed at this place, but that the functional persistent tooth is the milk tooth.

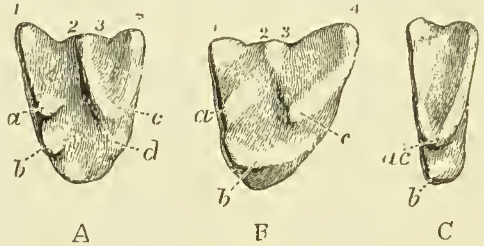
The Insectivora may be divided into groups by the pattern of their molar teeth: the majority present a W-pattern (Tupaia, Macroscelis, Erinaceus, Sorex, Talpa), whilst the other group have narrower molars with a V-pattern (Potamogale, Centetes, Chrysochloris).

The V-shaped tooth, having the early generalised tritubercular form, occurs in the Insectivora of Africa, Madagascar, and the West Indies only; it is probable that these are the more generalised types, and that those with the **W**-shaped molars are the more specialised forms.

The **W**-pattern met with in the molars of Insectivora is well exemplified in the molar of Urotrichus.

Mivart (Osteology of Insectivora, "Journal of Anatomy," 1868) held that the pattern of Insectivorous teeth were arrived at sometimes by a process of addition, new cusps being formed by elevations of the cingulum, so that the molars come to bristle with cusps, or by a process of lateral compression, the tritubercular tooth of the Cape Mole thus being due to a fusion of the more numerous cusps of such forms as the Mole.

FIG. 231 (1).



The trituberculate forms are said to approach the Jurassic trituberculata, but, as pointed out by Woodward, this hardly applies to the lower teeth; and it is noteworthy that Woodward finds in the two genera which he has examined that the protocone is the first cusp to appear, both in the upper and the lower jaw. But though this fact is one which will be gratifying to the advocates of the tritubercular theory, unfortunately it is not true of other genera; for those Insectivora which have more complex upper teeth, with four or five cusps, present a totally different order of appearance of the cusps, and the paracone and metacone appear first. Indeed, it is true of all mammals, except the two mentioned, which have been adequately examined, that the paracone appears first in the upper teeth, the protocone coming second or third in order.

This suggests that the homologies, as set forth by Osborn and Cope may not be correct, but that the so-called Paracone in the

(1) Upper molar teeth of (A) Urotrichus; (B) Mole; (C) Chrysochloris. (After Mivart.) The four principal cusps, according to Mivart, are lettered *a*, *b*, *c*, *d*, the other cusps being elevations of the cingulum. Woodward would suggest as their homologies: *b*. Protocone. *a*. Paracone. *c*. Metacone. *d*. Hypocone. He therefore agrees with Mivart that the additional cusps upon the outer border are of less importance than the other or inner four.

upper molar is the real Protocone. If this be so, the awkward dilemma, that in the premolars of various mammals the protocone stands outside, and that in the molars it stands inside (Scott, "Proc. Nat. Sc. Philad.," 1892), much alike though the last premolar and first molar may be, would be got rid of.

Dr. Forsyth Major ("Annals and Magaz. Nat. Hist.," Dec., 1897) gives strong reasons for not regarding the tricuspid teeth of Chrysochloris and Centetes as primitive forms; but, on the contrary, as due to reduction, thus re-asserting Mivart's view and rejecting those of the advocates of trituberculism so far as these teeth are concerned.

He holds that in the upper molars the three cusps present are certainly not the three cusps of the primitive triangle or trigon, but that the paracone and metacone are fused together, and that the protocone is greatly reduced. He further remarks that in the interpretation of the homologics the cusp, which is really paracone + metacone, has been pretty generally confounded with the protocone. The lower molar on the contrary he regards as consisting essentially of the primitive triangle.

He considers that on close examination and comparison with other forms, the so-called tritubercular molars contain more components than the three cusps, and that the three main cusps with which he is dealing have *different homologies* in each of the three orders (Lemuroidea, Carnivora, Insectivora) with which he deals; hence he regards these sporadic appearances of trituberculism as phenomena of convergence.

In a paper upon the great extinct Lemuroid Megaladapis ("Phil. Trans.," 1894), he points out that both this creature and Centetes have tritubercular upper molars, but that when we come to look at the lower molars we find that in the one it is the front part of the tooth which has undergone reduction, whilst in the other it is the back or heel. Now, according to the advocates of trituberculism, this heel or talon is a secondary and later introduction, but this he entirely disputes.

In support of his argument that the tritubercular molar is a tooth which has been reduced, he cites the fact that Viverridæ, Centetidæ and Lemuridæ all have it, though there can hardly be any close genetic relationship between them, and there is, moreover, evidence that the reduction sometimes goes on well beyond the stage of trituberculism in each of these families, *e.g.*, in the carnivorous Eupleres, the Insectivorous Hemicentetes, and the Lemuroid Chiromys.

The structure of the teeth of Insectivora does not call for much detailed notice. Penetration of the enamel by dentinal tubes occur in some—*e.g.*, Sorex.

In the Shrews the outer layer of the enamel is deeply pigmented. The enamel is abundantly entered by dentinal tubes, and there is no sharp line of demarcation at the junction of the two tissues; the tubes in the enamel often bend abruptly and then resume their original direction.

In Erinaceus the tubes do not enter so freely, nor do they run far in the enamel.

In Gymnura and Tupaia there is little sign of penetration, and the dentinal tubes break up into brushes at the edge of the dentine.

In Galeopithecus and Centetes no penetration occurs, but the enamel is very distinctly laminated.

In Galeopithecus there is a distinct granular layer underneath the enamel, but in no other Insectivora which I have examined does a granular layer occur in this situation; this is probably correlated with the frequency of penetration of the enamel by a tube system, and in this respect, as well as in many others, Galeopithecus stands somewhat apart from the other members of the group.

THE TEETH OF CHIROPTERA.

The Bats, sharply distinguished from all other mammals by the possession of wings, are divided into two groups, respectively insectivorous and frugivorous.

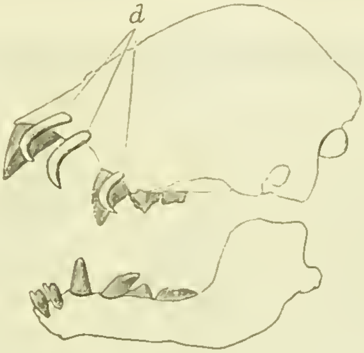
The insectivorous Bats, by far the most numerous section, are for the most part possessed of small incisors, rather large canines, and premolar and molar teeth which bristle with sharp cusps, and generally present the **W**-pattern. In fact, in general character, their teeth resemble those of the Insectivora, but the dental formula never exceeds—

$$i\,\frac{2}{3}\;c\,\frac{1}{1}\;pm\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The incisors are sometimes reduced in number, and spaces left between them; and some, as for example, the Vampire **(Desmodus)**, have teeth specially modified to accord with their blood-sucking habits.

This Bat has only one permanent incisor on each side, and this is a large but thin and sharp-edged tooth, with which the wound is made; the lower incisors are small teeth with feebly notched edges. The canines are large, and the molar series, which is not required in an animal existing upon blood, is stunted. The molar teeth are, however, sharp, though small, and there is no marked distinction into molars and premolars: the dental formula is—

Fig. 232 (1).



$$i\ \frac{1}{2}\ c\ \frac{1}{1}\ pm\ \frac{2}{3}\ m\ \frac{0}{0}\ \text{or}\ \frac{1}{1}.$$

The frugivorous bats (of which the **Pteropus**, or flying fox, is an example) have much larger muzzles, and the molar teeth are set with intervals between them.

The dental formula is $i\ \frac{2}{2}\ c\ \frac{1}{1}\ pm\ \frac{2}{3}\ m\ \frac{3}{3}$, but in some the molar series is reduced below this number.

The incisors are small, and the canines rather large.

Both molars and premolars are of somewhat simple form, being long, and compressed from side to side. The outer borders of the crown of the molars are elevated into distinct but not exceedingly sharp cusps, which become worn down by use.

The insectivorous character of the presence of many sharp cusps upon the teeth is not to be found in any of the frugivorous bats. All the Pteropi have deciduous canines, and four deciduous molars, of simple pointed form, but the number of deciduous incisors is very variable.

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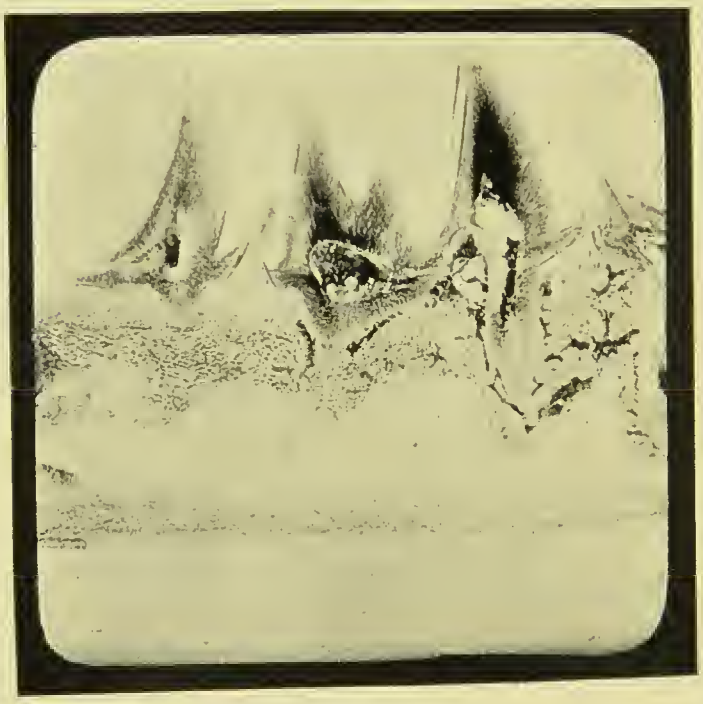
(1) Skull of Desmodus, showing milk teeth.

The milk dentition of bats has been very carefully and thoroughly investigated by Leche ("Lunds Universit. Arsskrift," tom. XII. and XIV., 1878), and at the present the Megadermata are the only family in which the milk teeth are unknown. The milk teeth are not of much functional importance, as they are shed soon after, if not absorbed before, birth, and they are not therefore implanted in very definite sockets.

Fig. 233 (1).



In their slight cylindrical elongated roots, surmounted by expanded crowns, these milk teeth often recall those of the Mole.

Sometimes the milk teeth are to be found even after the permanent teeth are *in situ;* in other instances, as for example the deciduous molars of Molossus, they never cut the gum. The milk dentition of the Vampire (Desmodus) (1) appears to consist of incisors only, or of incisors and canines; though the absence of observed molars may be due to the fact that they are, as in Molossus, shed very early.

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(1) Section of molar teeth of Rhinolophus *in situ*, with extreme development of cingula.

It has, near to the front of the upper jaw, six teeth, each of which is very long and slender, and has a strongly hooked point: it has been suggested that these feeble hooked teeth may assist it in holding on to the mother.

In general terms it may be said that the milk teeth of the majority of Chiroptera do not at all resemble their permanent successors.

An anomalous dentition has been found in a Solomon Island Bat, in which the canines, whilst having a long principal cusp, are rendered multi-tuberculate by other cusps at their base, this pattern being more or less repeated in the other teeth. (Oldfield Thomas, " Proc. Zool. Society," 1889.) This seems to indicate that the fruit-eating bats are descended from Insectivorous forms.

The bats illustrate well a character of Insectivorous dentition in the production of the cingulum to such an extent as to completely cover and protect the gum between the teeth.

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(1) In a skull of Desmodus, in the possession of Mr. R. F. Tomes, the third milk tooth appears to correspond in position to the permanent canine; the same is the case in the specimen figured by Messrs. Gervais and Castelmain (Expéd. dans les part. cent. d'Amérique du Sud).

CHAPTER XIV.

THE TEETH OF PRIMATES.

The order Primates embraces Man, Monkeys, and the Lemurs.

Some naturalists have been disposed to separate the Lemuridæ from the rest of the Primates, on the ground that some Lemurs approximate rather closely to the Insectivora, while again the order Insectivora contains some forms which recall the Lemurs.

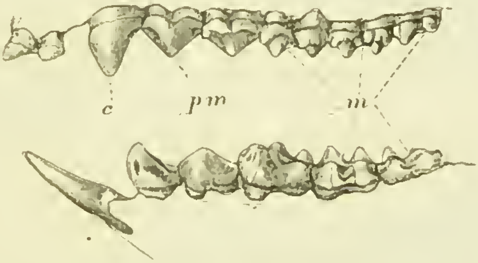
Professor Cope regards the Lemurs as an exceedingly ancient and generalised form, and considers that they may have been parent forms of many widely different mammalian forms.

But although the Lemuridæ are undoubtedly inferior to the Monkeys, and stand apart from them more widely than do the Monkeys and Man, most authors now place them in the order Primates, which is to be divided as follows :—

Primates	Lemuridæ.	Lemurs.
	Simiadæ.	Old and new-world Monkeys.
	Anthropidæ.	Man.

Lemuridæ.—The Lemurs, for the most part are found in Madagascar, and to a less extent on the mainland of Africa and in southern Asia, though in the Tertiary Eocene period they were far more widely distributed. In their dentition, just as in other characters, they differ somewhat from the true monkeys, though, on account of there being several very aberrant in form, it is difficult to give any general account of them, the more so as their dentitions vary much more than does their food, so far as it is known. Most Lemurs eat insects, reptiles, small birds, and fruits. Generally, the upper incisors are very small, and widely separated from one another ; in the lower jaw these are antagonised by six or eight long, thin, narrow procumbent teeth, generally regarded as being two pairs of incisors and the lower canines, though some regard them as all being incisors and the lower canine as being absent: in both upper and lower jaws the next tooth is large and pointed like a canine, but the lower caniniform tooth bites behind the upper, and so is held not to correspond to it, but to be the first premolar. In this respect they differ from the Monkeys, in whom the lower caniniform tooth is the same tooth as in man, but it is interesting to find that in the fossil forms this difference does not exist, so that Lemurine forms may easily have been the ancestors of the Monkeys proper, and hence especial interest attaches to them. The premolars are compressed from side to side, and are very sharp, while in many of them the lower premolars are two-rooted, the roots being more or less completely in the position of outer and inner, not of anterior and posterior roots. The molars are armed with long sharp cusps, which are worn down in old animals, and whilst the upper molars in many lemurs are armed with four cusps, the upper and lower molars being very generally alike, a three-cusped molar of tritubercular form is the one most typical of the group, and is general amongst the extinct species; the latter also present some examples of the full mammalian number of four premolars, and so were, in many particulars, much less specialised than their recent descendants.

FIG. 234 (¹).



(¹) Teeth of the Indri.

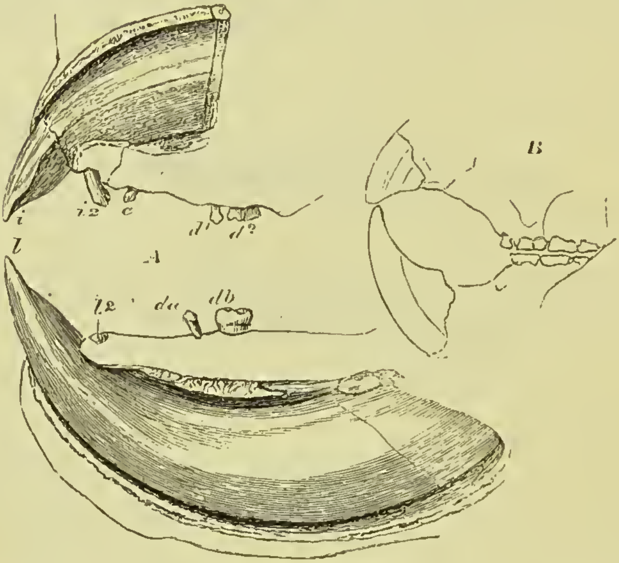
The Indri, the largest of the Lemuroids, has

$$\text{i}\,\frac{2}{1}\;\text{c}\,\frac{1}{1}\;\text{pm}\,\frac{2}{2}\;\text{m}\,\frac{3}{3},$$

$$\text{or i}\,\frac{2}{2}\;\text{c}\,\frac{1}{0}\;\text{pm}\,\frac{2}{2}\;\text{m}\,\frac{3}{3}.$$

In it there are fewer teeth than in the true lemurs, there being only one incisor in the lower jaw; and as the canine ranges with it, the upper canine is antagonised by a two-rooted, pointed tooth which closes behind it, and is a premolar; in the milk dentition there are two additional teeth in the fore part of the lower jaw, one apparently the true canine, and the other a premolar.

FIG. 235 (¹).



The premolars are compressed and pointed, and the true molars are quadri-tubercular. It has been suggested by Cope that the procumbent position of the lower incisors, which do

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(¹) Upper and lower jaws of Chiromys. A. Milk dentition, with the permanent incisors just emerging. *i*, *l*. Upper and lower permanent incisors. *i* 2, *l* 2. Upper and lower milk incisors. *c*. Milk canines. *d* 1, *d* 2, *d a*, *d b*. Upper and lower milk molars. (Twice natural size.) B. Reduced figure of permanent teeth. (After Peters.)

not accurately oppose the upper incisors, may have been acquired by the animal's habit of combing its fur with these teeth. ("Primary Factors of Evolution (Kinetogenesis)," p. 326.)

In the Lemurs proper there are thirty-six teeth, their dental formula being usually written

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}.$$

The lower canine is procumbent, ranging with the incisors, and may be counted as a third incisor.

In some of the Lemuroids the upper incisors are further reduced (Lepidolemur has them absent or rudimentary, and Nycticebus has often only one), whilst in the very aberrant **Aye-Aye (Chiromys)** the incisors are enormous, so that its dentition imitates the rodents—

$$i\,\frac{1}{1}\;c\,\frac{0}{0}\;pm\,\frac{1}{0}\,m\,\frac{3}{3}=18.$$

In both upper and lower jaws the incisors form a single pair of large curved teeth, growing from persistent pulps, and wearing obliquely so as to constantly preserve a sharp cutting edge. The enamel is very much less thick, if not altogether absent, upon the backs of the upper incisors, but the lower incisor, which is very narrow from side to side, and very thick from back to front, is composed very largely of enamel, the dentine constituting but a small part of it.

After a considerable interval, which is devoid of teeth, there follow four upper and three lower teeth, which are not of persistent growth, but have definite roots, and resemble the molars of many omnivorous rodents.

Although, functionally, its teeth are those of a rodent, yet despite this adaptive resemblance, the milk dentition retains certain characters which indicate the lemurine origin of the creature.

In the upper jaw the milk dentition consists of two small incisors, a canine and three molars; in the lower jaw of two small incisors and two small molars; it is said that in an early stage a third milk incisor is to be found—

$$\text{di}\,\frac{2}{2}\,\text{dc}\,\frac{1}{0}\,\text{dm}\,\frac{2}{2}.$$

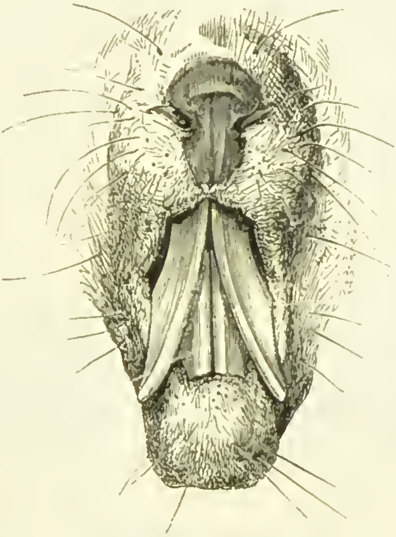
The permanent incisors push their way up between the first and second milk incisors; at a certain stage all three are to be seen at once, but the large size of the permanent incisors causes the speedy loss of the milk incisors.

No known rodent has so many well developed milk teeth; the Aye-aye thus affords an excellent example of a milk dentition preserving characters which are lost in the extremely modified adult dentition.

Being a somewhat rare and strictly nocturnal animal, little is known of its food; some have believed that it made use of its rodent incisors to cut away portions of wood in order to get at the grubs contained in it, drawing them out of their hiding-place by means of its curiously elongated finger, whilst others believe that it gnaws the sugar-cane. One specimen kept in confinement had the habit, no matter what it had been eating, of passing each of its long fingers carefully through its mouth after finishing its food, as though these fingers were apt to get soiled in the getting of its natural food. But whatever the nature of its food may be, it is certain that its scalpriform incisors are put to hard work, and so kept worn down, for in a specimen kept for a time in the Zoological Gardens, which was supplied with soft food, the incisor teeth grew to an excessive length, and ultimately caused the animal's death by the points of its lower incisors perforating the palate. The accompanying figure represents the muzzle of this specimen, and although the upper teeth have grown to an inordinate length, and have diverged from one another, it will serve to show the rodent-like aspect of its mouth.

The special interest which attaches to the dentition of Chiromys has been already alluded to; to briefly recapitulate, it is this: in Madagascar, an isolated area separated by a wide tract of deep sea from other areas, true rodents are almost absent, but lemurs abundant. But one of the lemurine animals which are to be found there has been so modified that its teeth to all intents and purposes are those of a rodent. Yet with all this modification it retains characters (notably its milk dentition) which are quite unlike those of true rodents, but which recall the manner of its origin from higher lemurine forms.

FIG. 236 (1).



Simiadæ.—The true monkeys are divided into two great divisions, the new-world monkeys and the old-world monkeys. The former differ in many respects from the latter; for the most part they have prehensile tails, and their nostrils are set somewhat widely apart, whence they are called *Platyrrhine*, or wide-nosed monkeys, and they differ also in their dental formula, which is—

$$i\,\frac{2}{2}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{3}{3}\;=\;36.$$

They are divided into Hapalidæ (Marmosets) and Cebidæ.

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(1) Aye-Aye (Chiromys), which died in the Zoological Gardens. (After Dr. Murie.) The upper incisors, from want of sufficient use, have grown long and diverged from the middle line.

The little **Marmoset** monkeys have only 32 teeth, but they still agree with the other new-world monkeys in having three premolars on each side, the molars having been reduced to two in number. The upper molars of some new-world monkeys, notably Ateles and Mycetes, have the antero-internal and extero-posterior cusps joined by an oblique ridge, a character which is shared in the old-world groups by man and the anthropoid apes only.

In the Cebidæ the molars have very sharp cusps, as in the Insectivora, and the upper and lower molars are not alike.

In the spider monkeys (**Ateles**) the outer lower incisors are caniniform, and the canines, which are long and sharp, are very like the anterior premolars, but have their outer cusps much longer. The inner cusp of the anterior lower premolar is hardly developed, but in pm_3 the inner cusp and posterior cingulum is more pronounced, and in pm_4 it is yet more strongly expressed; they are all single-rooted, and show the relationship of the canine to the premolars excellently well. (See p. 539.)

The upper premolars, especially the last, have roots bifurcated near their tips, but have not three roots. The bifurcation in the root of m_1 takes place only low down, in m_2 lower still, and m_3 is single-rooted and small, so that the teeth show a tendency to reduction.

Of the upper molars the first two are three-rooted, but the third is hardly even bifurcated.

All Quadrumana have well-developed milk dentition.

Old-world or *Catarrhine* monkeys all have the same dental formula as man—

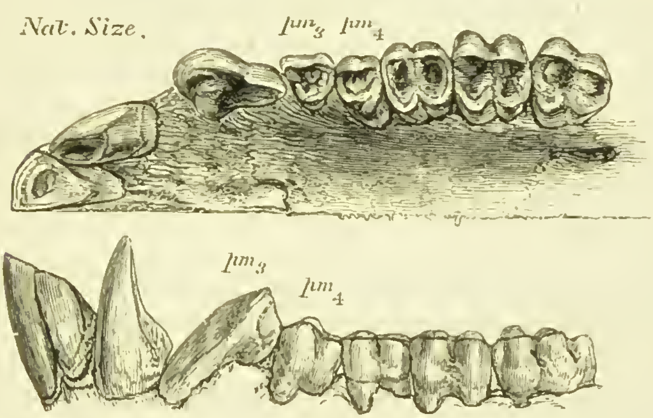
$$i\,\frac{2}{2}\ c\,\frac{1}{1}\ p\,\frac{3}{3}\ m\,\frac{3}{4}.$$

They have nipple-shaped cusps to the molars, as in man and the Anthropoid apes, but in the Pithecidæ the upper and lower molars are alike. As an example the **Macaque** monkey may be taken. The upper and lower incisors, but especially the former, are directed obliquely forwards, and the lateral incisors are very much smaller than the centrals. In the upper jaw a considerable interval separates the incisor from the canine, which is a very large tooth, somewhat triangular in section, with a sharp edge directed backwards, and with a deep groove on its anterior surface.

The upper premolars are implanted by three distinct roots, as are also the true molars; the latter are quadricuspid, but lack the oblique ridge.

The lower canine is a sharp and powerful tooth, though it is very much smaller than the upper; the first lower premolar, by its front surface, articulates with the upper canine, and is of curious form. It is implanted by two roots, but the anterior root is produced forwards, so that the antero-posterior extent of the tooth is much increased.

Fig. 237 (1).



The apex of the cusp of the tooth is almost over the posterior root, and from this point the crown of the tooth slopes obliquely forwards down to its anterior root. This peculiarity in the form of the first lower premolar is eminently characteristic of the baboons. There is nothing to note of the second premolar save that it is implanted by two roots, like the true molars, which are quadricuspid;

---

(1) Upper and lower teeth of a monkey (Macacus nemestrinus, male). The length and sharpness of the canines, and the peculiar form of the anterior lower premolar, contrast with the aspect of the corresponding teeth in the Anthropoid apes or in man.

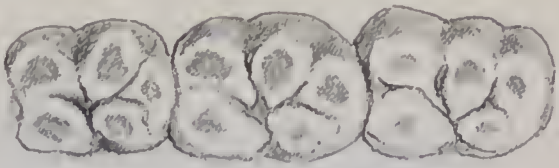
of them the third is larger than the first two, and is quinquicuspid.

But in some genera, *e.g.*, Cercopithecus, this is reduced in size and is tricuspid.

There is considerable difference in the size of the canine in the two sexes, that of the male being very much the larger; this difference does not exist in the deciduous dentition, in which the canines are relatively small.

The Anthropoid Apes include the Gibbons (Hylobates), the Orang (Simia), the Gorilla (Gorilla) and the Chimpanzee (Anthropopithecus, formerly called Troglodytes); all of them have the oblique ridge upon the upper molars.

FIG. 238 (¹).



Upon the whole the gibbons are the lowest, and the gorilla or the chimpanzee the highest of the anthropoid apes, which are all confined to tropical areas. Thus the gorilla and chimpanzee are confined to tropical Africa, and the orang is limited to a part of the Malay archipelago. The gibbons are more widely distributed over the Malay archipelago and tropical Asia; their teeth are not unlike those of man, except that their longer, slender canines extend far above the level of the other teeth.

Although the **Gorilla** on the whole approaches most nearly to man, this can hardly be said to be the case with its dentition. The jaws are very square, and there is a large diastema in front of the upper canine, which in the male gorilla is of great size and strength, its top descending far below the level of the alveolar border of the lower jaw when the mouth is shut.

In the lower jaw there is no diastema, but the teeth are

(¹) Slightly-worn lower molars of a gorilla, showing the arrangement of the five cusps.

all in contact with one another: the first of the premolars is a very strong pointed cone, showing plainly the close relationship between canines and premolars alluded to at a previous page.

The molars increase in size from before backwards, the third molars attaining to a very large size, and in the lower jaw all three have five cusps.

Nevertheless, though the teeth are coarser and stronger, there is a general resemblance to those of man.

It has been pointed out by the late Professor Rolleston that the canine tooth of the male anthropoid apes is a little later in coming into place than in the female. Thus in the male chimpanzee and orang, it is not cut until after the third molars (wisdom teeth) are in place, whereas in the female it follows the second, but precedes the third molars. The sexual difference in the canine teeth is very well marked in all the anthropoid apes, and its later eruption in the males is explicable both upon the ground that, being a sexual weapon, it is not needed prior to the attainment of sexual maturity, and also that, being of very large size, its formation might be expected to take a longer time. No such difference pertains to the milk dentition, in which the order of eruption is exactly that which is met in man.

Dr. Magitot ("Bulletin de la Société d'Anthropologie de Paris," 1869) combats the idea that there is any difference in the order of the eruption of the permanent teeth between man and the anthropoid apes, but, while his observations have been both careful and widely extended, he lays much stress upon an observation made upon a *female* gorilla skull, in which, as has just been mentioned, the order of succession is not quite the same as in the male.

In a specimen of a New World Monkey (Cebus hypoleucus) I have found m_3 on the point of erupting, whilst the temporary milk molars had not yet been shed, and the canine was not yet erupted.

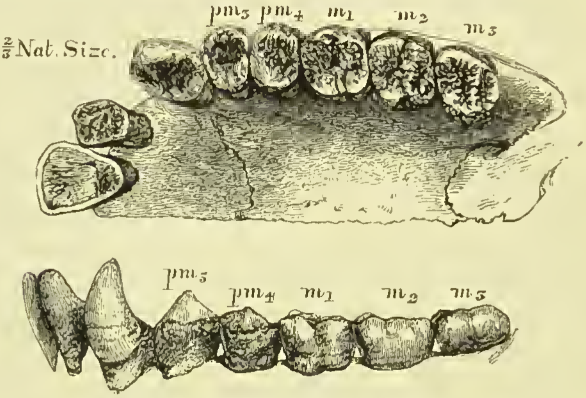
Sir W. Flower says in general terms that the canines are the last teeth to be cut, but mentions that in the gibbons they come up at the same time with, or even precede, the third molar, and this is also sometimes the case in the orang.

Giglioli says that in a chimpanzee the order is the same as in man, but that in a male gorilla he found the canines and third molar erupting simultaneously, the former teeth, however, taking the longest time to fully erupt.

The dentition of the **Orang** approaches tolerably closely to that of man, and the points of resemblance and of difference may be fairly well seen in the accompanying figure.

The central upper incisors are similar to those of man, but are larger; the laterals are, relatively to the centrals, much smaller, and are very caniniform in shape, both inner and outer angles of their cutting edge being sloped off to such an extent that a central-pointed cusp remains, in place of a thin cutting edge. The canines are strong, pointed teeth, the cingulum and the ridge joining it with the apex of the cusp being well marked upon their inner sides. In the female the upper canine is about half as long again as any of the other teeth: in the male it is longer.

Fig. 239 (1).



The first bicuspid is a little more caniniform than that of man; its outer cusp is long and pointed, and a ridge unites it with the anterior part of the inner cusp, which is feebly pronounced; the second is a blunter and broader tooth.

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(1) Upper and lower teeth of an Anthropoid ape (Simia Satyrus, or Orang Outan).

The premolars are implanted by three roots. The molars are not unlike the human teeth in pattern.

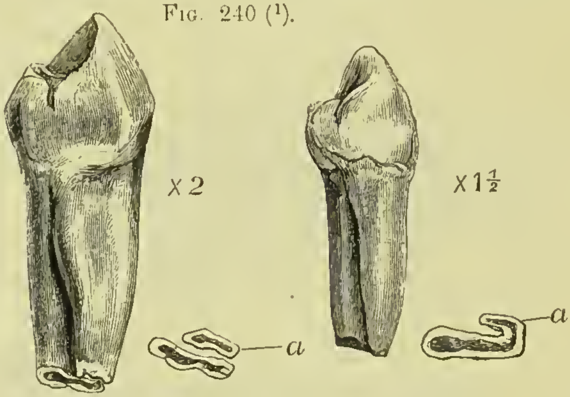
In the lower jaw the incisors are large and stout; the canines sharply pointed, with a well-marked cingulum, and a well-marked median ridge on the inner side of the crown. The first premolar is a shorter, stouter, and blunter copy of the canine, and can hardly be said to have an inner cusp. In the second premolar the inner cusp is as high as the outer, and the cingulum is elevated both before and behind till it almost forms two additional cusps, but both teeth have two distinct roots which lie anteriorly and posteriorly like those of the lower molars. Indeed, I am not acquainted with any dentition which exemplifies the transition from incisors to canines, from canines to premolars, and from premolars to true molars, better than that of the orang.

There is also a point of interest about the lower premolars which may be noticed here. If the lower first premolar of one of the anthropoid apes be examined it will be found that its posterior root occupies the whole width of the alveolar border, but the anterior root though when looked at from above is found to be of much less width, and it does not extend inwards to much more than half the distance reached by the posterior root.

There is a form of abnormal root which is met with in the first lower premolar of man, of sufficient frequency of occurrence to obviously have some significance, which consists in the outer border of the root towards its apex being folded forwards and inwards, so as to present an approximation to a double root at the end. I have myself collected eighteen examples of this, and in two it has gone to the extent of a second small anterior root being completely formed.

Thus we have as a comparatively common abnormality a tendency to the formation of two roots, one anterior and the other posterior, and in every single instance it is the posterior root which is fully developed, and the anterior root is tending to be formed as a smaller root, on the outside quite level with the other, but not extending inwards in the direction of its width to nearly the same extent as the posterior root. In fact it is trying to parallel the state of things which is constant in most anthropoid apes, and is hardly explicable on any other hypothesis than that it is a reversion, for in a reduced dentition like that of a xanthocroic man it is not conceivable that there should be a tendency to the development of a second root to the first premolar as a commencement of a new order of things.

Fig. 240 (1).



The lower molars resemble those of man, save that their surface is marked by that finely-wrinkled pattern which is common to all the unworn teeth of the orang. One is struck by the great backward elongation of the jaws, by their squareness, by the parallelism of the two sides, which converge slightly at the back, and by the large size of the teeth in proportion to the bulk of the whole animal.

The large size of the canines being in a measure a sexual character, is, as is so often the case, not very noticeable in the young animal: the two accompanying illustrations of a young and an adult male orang may serve to show this, as well as some other differences developed by age.

A peculiarity of the orang lies in the enormous length of the roots of its teeth; this is not shared by the gorilla, the roots of whose teeth are proportionately shorter, and the chimpanzee has roots far shorter and feebler than either.

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(1) Lower premolar (human). In the right-hand figure a second (anterior) root is in process of formation by a folding round of the flattened end of the root; in the left-hand figure it has attained to being a distinct root.

Fig. 241 (¹).

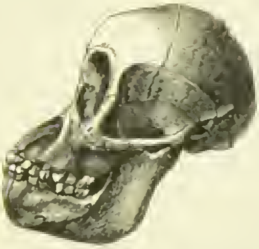


Fig. 242 (²).

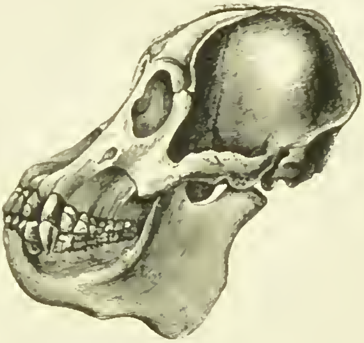
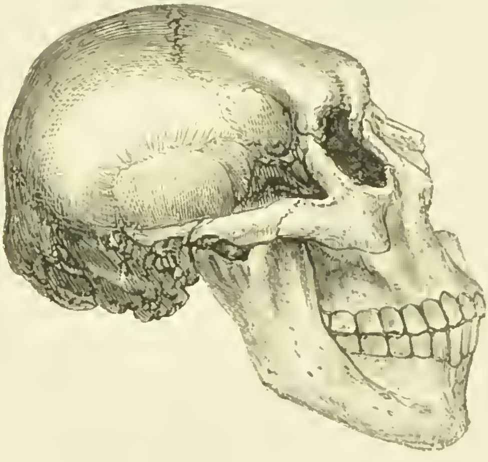


Fig. 243 (³).



Looking at the palatine surface of the jaws of an orang, the front of the mouth is squarish, and the premolars and molars stand nearly in a straight line, not, however, strictly parallel with those of the opposite side, as they approximate

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(¹) Skull of a young male orang. The upper canine does not nearly reach to the lower alveolar border.

(²) Skull of adult male orang, in which the canine is largely developed.

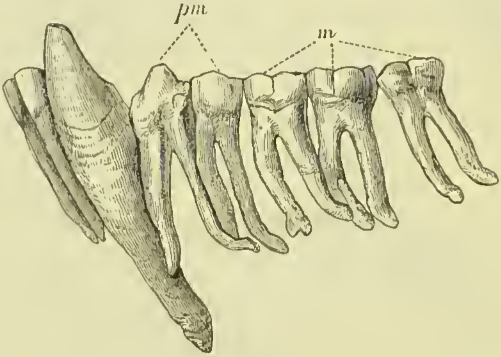
(³) Side view of skull of an idiot.

at the back, the third molars being nearer together than the premolars. In the gorilla the two sides of the "arch" are parallel, and in the chimpanzee they are also nearly parallel, with a slight approximation at the back.

So far as teeth go the chimpanzee most nearly resembles man: the canines are not so large, and there is no very great sexual difference in the canines, and none in the general size of the whole animal.

The teeth of the **Chimpanzee** are not very powerfully developed, and the third molars are a good deal smaller than the other teeth; the lower premolars also have their two roots more or less fused.

FIG. 244 (1).



The upper premolars are shorter in antero-posterior extent than those of other anthropoids, their outer predominate over their inner cusps, and in their position relatively to the molars they more closely follow the human type.

Another difference between the chimpanzee and the orang and gorilla lies in the comparatively early closure of the intermaxillary suture: this suture closes in man about the time of birth, in the chimpanzee about the time of the change of the teeth, whilst in the orang and gorilla it remains permanently open. Hence there is a greater capacity for forward elongation or increased prognathism in the latter, and in the chimpanzee than in man, and this is related to the great size of the canines and the formation of the diastema which hardly existed in the temporary dentition.

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(1) Lower teeth of Orang. From a jaw from which bone had been removed exposing the roots of the teeth to their ends.

There would appear to be a great deal of variability about the articulation of the upper and lower teeth in the higher apes.

Thus in the British Museum there are three orangs which are distinctly underhung, and several whose incisors present an "edge to edge" bite. There are also three underhung chimpanzees, as well as one which is underhung in the milk dentition, a thing exceedingly rare in man. There is also an underhung gorilla; and in the museum of the Odontological Society there is a gorilla's skull in which the lower jaw contains two supernumerary teeth buried in the substance of the ascending ramus, with their crowns looking upwards, close to the foramen where the inferior dental nerve and vessels enter the bone. ("Odonto. Soc. Transac.," Vol. XIX., 1887.)

There is a good deal of variability in the number of teeth in anthropoid apes, no less than 8 per cent. of the skulls examined by Bateson ("Proc. Zool. Soc.," 1892) having supernumerary teeth: he, however, found no examples of these in the gibbons; in Cebidæ and Ateles he found them in 4 per cent., and in other new-world monkeys he found none at all.

The differences which serve to distinguish the dentition of the most anthropomorphous apes from that of man are mainly these. Relatively to the size of the cranium, and of the whole creature, the teeth and jaws are very much larger in all their dimensions; hence the creatures are prognathous, and the facial angle small, even when compared with the jaws and cranium of an idiot. As might be expected, this difference is not so great in the young as in the adult animal.

In place of the teeth being arranged in a sweeping curve, the jaws are squarish, the incisors being arranged in something approaching to a straight line between the two great outstanding canines, behind which the premolar and molar series run in straight lines, converging somewhat as they go backward. There is a "diastema" (1) or interval in front of the upper canine, into which the point of the lower canine passes, when the mouth is closed. Both the greater squareness of the jaws, and the existence of a diastema, are direct results of the great size of the canines, and are consequently not marked in young specimens.

The upper premolars are implanted by three roots, the lower by two roots, just like the true molars, and the premolars when unworn partake more of the pointed character than they do in man.

The wisdom teeth present the same pattern of cusp surface, are larger than the other molars in the gorilla and the orang, and there is abundant space for them, so that they play an important part in mastication. The molar teeth of these apes are also squarer, their cusps sharper and longer, and the characteristic patterns more strongly pronounced, than in man. Moreover, the intermaxillary bone is more largely developed, and the intermaxillary suture remains distinct through life, except in the chimpanzee.

Anthropidæ.—In passing from the highest of the apes to the lowest of mankind, there is a somewhat sudden change in the character of the dentition; but while it cannot but be admitted that there is a gap, yet the differences are all rather of degree than of kind.

As the canine is less largely developed, there is no diastema nor any sexual difference in dentition; no tooth projecting beyond its fellows, so that the teeth are arranged in an unbroken arch. The premaxillary bones become fused with the superior maxillary soon after birth, whereas in the chimpanzee they become fused by the completion of the second dentition, and in the gorilla and orang they remain distinct.

It is generally said that in man the molars decrease in size from before backwards; that is to say, that the first molar is the largest, while in anthropoid apes, with the exception of the chimpanzee, the contrary is the case.

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(1) Something approaching to a diastema is said to have been observed by Vogt and Broca in early European skulls.

Though this is on the whole true, it requires some qualification: thus in certain lower races, such as the Australian blacks, the second and third molars are not smaller than the first, and in the palæolithic man of Spy they are actually larger.

Palæolithic man was also characterised by a want of chin, so that a section of the lower jaw at the symphysis slopes backwards, and resembles that of an anthropoid ape.

One of the features by which the lower races of mankind differ from the higher, and resemble so far the anthropoid apes, is the prominence of the lower part of the face, in fact, in the large development of face as compared with cranium. The degree of prognathism, as this is termed, may in a rough way be described as being the amount by which, the skull having been placed in its normal position, the lower part of the face projects beyond a vertical line dropped from the forehead.

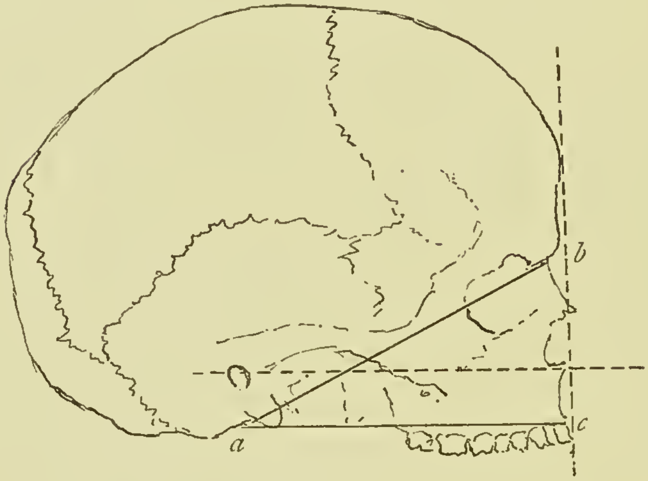
But such a rough method would be obviously unsuitable for comparisons and measurements, so Camper many years ago devised a method of measuring what was termed the facial angle. He drew a line through the external auditory foramen along the floor of the nose, producing it beyond the nares. A second line was drawn from the forehead between the supraorbital ridges down to the edges of the incisor teeth, this line crossing the first near where it emerged from the nares; the angle included between these lines at their intersection was called the facial angle. This gave about an angle of 20° for a dog, 85° for an Australian black, 95° for a European, and the Greeks used an angle of 100° or more to express their ideal of beauty and of intellectual power.

Camper's facial angle gave a general degree of prognathism which might, perhaps, be largely due merely to the inclination of the teeth, or be influenced, as in the gorilla, by the size of the supraorbital ridges; and almost every conceivable variety of points of measurement has been used by one or other observer, so that "facial angle" gives no precise information unless the parts of measurement are specified.

Jacquart took Camper's horizontal line, but drew his vertical line from the forehead to the centre of the lower edge of the alveolar border, thus eliminating the influence of the teeth themselves, but comparative measurements taken on these lines gave such small differences of angle that they did not seem worth the trouble of taking and recording. Others drew their horizontal line from the point between the occipital condyles along the floor of the nose; others from the auditory foramen obliquely down to the points of the teeth, &c.

The discrepancies due to the almost infinite variety, within small limits, of the points chosen led to anthropologists somewhat unduly neglecting the facial angle, and it is now generally differently expressed.

Fig. 245 (1).



A line may be drawn from the middle of the front margin of the occipital foramen (basion of Broca), to the root of the nose (nasion of Broca), and measured. This, of course, can be done on an intact skull by means of well-bowed callipers, and is called the Basionasal length.

A second measurement is taken from the same point (basion) to the middle of the front edge of the alveolus: this is called the Basi-alveolar length.

The former being taken as 100, the so-called alveolar index, or gnathic index, is got by multiplying the basi-alveolar length by 100, and dividing by the basionasal length,

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(1) Diagram of two of the methods of estimating the facial angle. The dotted lines represent those suggested by Camper, the full lines those along which measurements for ascertaining the gnathic index are taken.

$$\frac{\text{Basi-alveolar length} \times 100}{\text{Basionasal length}} = \text{Gnathic Index},$$

and the results thus set down—

Orthognathous, when it is below 98.
Mesognathous, when it is 98·1 to 103.
Prognathous, when it is above 103.

This method, due to Sir William Flower, seems the most satisfactory and is largely adopted, but unfortunately there is still a want of unanimity amongst anthropologists, and others are still met with, for which the reader must be referred to manuals of Anthropology.

Although it is true that the lower races of mankind are more often prognathous than the higher, yet it is not universal with them. The few palæolithic skulls which have been found are prognathous, but the Veddahs of Ceylon (a very low race), the Andaman Islanders, and the Bushmen, are all orthognathous, so that it would appear that orthognathism had been attained by some otherwise low races and afterwards lost again, or else that these races are not upon the same direct line of descent as the somewhat higher races who are prognathous.

In some of the palæolithic men the prognathism, otherwise considerable, is, just as in the gorilla, diminished by the huge supraciliary ridges, and although the alveolar borders are prominent and the lower jaw massive, yet there is a falling away below this, as the chin was very feeble.

In the man of Spy, the molars increase in size as they go backwards, instead of diminishing, and their three roots are very distinct, characters which are Simian and are only shared by a few low races (*e.g.*, Australians), in which the last tooth is as big as the others. In Java, Dr. Dubois has recently found some fragments, apparently of Pleistocene Age, which may have belonged to a high form of anthropoid or a very low form of man, such as the Neanderthal skull. Cope regards the remains as human; the tooth being of character which might refer it to an anthropoid ape, or a low race of mankind, and the fragments of skull not unlike those of the Neanderthal man. The femur, which was entirely human, was met with about fifty yards away. On the whole we may say that in the Neanderthal man we have a greater number of Simian characters than exist together in any living man, though each of the characters may be met singly in other low types of mankind.

It seems possible that prognathism is related to the period of closure of the intermaxillary suture, for in the gorilla the antero-posterior length of the premaxilla increases from 19mm. in the period of complete deciduous dentition, to 22mm. in the female and to 27mm. in the male at the period of adult dentition; in the orang from 11mm. to 15mm. and 18mm., and in the chimpanzee from 8mm. to 14mm. and 19mm., whereas in man no growth takes place in this region. ("Studies on the Growth of the Jaws," C. S. Tomes, "Trans. Odont. Soc.," 1892.) No material is available for ascertaining whether the intermaxillary suture is late in closing in prognathous lower races of mankind, but it is noteworthy that persistence of the suture, though rare, is sometimes met with in them.

Almost the whole forward elongation is accounted for in the chimpanzee by the growth of the premaxilla, but this is not so in the orang and gorilla, in whom there is also growth of the edge of the maxilla. This elongation of the premaxilla and maxilla obviously has relation to the extent of the development of the canines, and of the formation of the diastema, being much greater in the males than in the females.

Hence in this respect, as in others, the deciduous dentition of anthropoid apes more closely resembles that of man than do their respective permanent dentitions, and the chimpanzee, with its short premaxilla, at the earlier period resembles man the most.

Of living races of mankind, it may almost be said that if we wish to find an absolutely typical human dentition, we should go to the lower races, as in the higher a process of reduction seems to be taking place.

In general terms it may be said that the dentition of the lower races of mankind differs from that of the higher in the following particulars: the arch is not so rounded, but is squarer in front; the teeth are larger, and are disposed with greater regularity; the wisdom tooth has ample space to range with the other teeth, and is a characteristic upper or lower molar, the pattern of its grinding surface (quadricuspid if it be an upper, quinquicuspid if it be a lower tooth) and the disposition of its roots corresponding with

Fig. 246 (1).

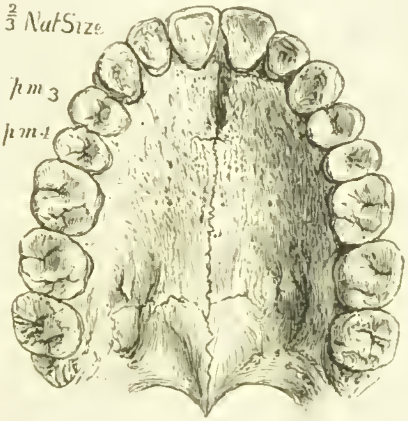
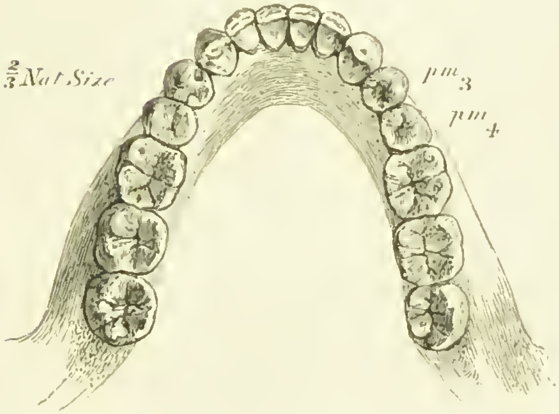


Fig. 247 (2).



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(1) Upper teeth of a Caffir. The oblique ridge of the upper molar is distinct, not only upon the first and second, but also upon the third molar or wisdom tooth, which in this skull has the normal three roots well marked.

(2) Lower jaw of a Caffir, in which the quinquicuspid form of the first and third molars is well seen, it being somewhat less strongly indicated in the second molars.

the first and second molars, which do not greatly exceed it in size. Specimens of negro skulls may be found in which there is scanty room for the wisdom tooth, and in which consequently it is a little stunted in its development: on the other hand, plenty of well-formed and well-placed wisdom teeth may be picked out of European mouths, though as a rule the wisdom tooth is much smaller than the other molars, does not bear the characteristic pattern of cusps and grooves, has its roots connate, and it is not very infrequently a mere rudimentary peg. The stunted development of the wisdom tooth would seem to be a consequence of want of space during its formative period; the upper wisdom tooth is especially apt to be cramped in this way.

There is some little evidence that the wisdom tooth is in process of disappearance from the jaws of civilised races: in anthropoid apes the wisdom tooth is nearly or quite as large as the other molars, and shows no variability, whilst it comes into place almost simultaneously with the canine: in the lowest races of mankind the wisdom tooth appears to vary but little, is of large size, and is seldom misplaced; in highly civilised races it is very variable in size, form, and in the date of its appearance, is often misplaced, and is not uncommonly quite rudimentary. It seems to be a legitimate inference that a further modification of the race in the same direction will result in the disappearance of the wisdom tooth altogether.

Some exception must, however, be taken to such general statements: thus the Esquimaux not uncommonly have the wisdom teeth small and sometimes crowded out of place; and amongst the African races instances on the one hand of the wisdom teeth being small, and on the other, of fourth true molars existing, are to be met with.

Nevertheless, for the present, a case in which the wisdom teeth are very small can hardly be called a typical well-developed European mouth.

It is stated by Regnault ("Soc. d. Biologie," 1893) that the upper incisors differ in the various races of mankind: in the white race their lateral borders are parallel, but they are divergent in negro races; so that the difference in width between the cutting edge and the neck is twice as great in the black races: this peculiarity exists also in the milk teeth, and is also traceable in the canines of both dentitions. The canines of lower races are generally very strong; and a slight diastema occasionally exists. Although man has ceased to use them as fighting weapons, yet there is a curious survival in an expression of the face, as is thus well put by Darwin, "He who rejects with scorn the belief that the shape of his own canines, and their occasional great development in other men, are due to our early progenitors having been provided with these formidable weapons, will probably reveal by sneering the line of his descent. For though he no longer intends, nor has the power, to use these teeth as weapons, he will unconsciously retract his 'snarling muscles' (thus named by Sir C. Bell) so as to expose them ready for action, like a dog prepared to fight." ("Descent of Man," p. 127.)

It has been pointed out by Sir Wm. Turner that besides the dental arches being both longer and broader in Australian skulls than in Europeans, the front teeth more often meet edge to edge instead of the lower passing well inside the upper incisors.

The cusp pattern of human molars has been a subject of interest to many observers, on account of its seeming to indicate in some degree the problems of human descent.

I began to make a record of the percentage of deviations in the cusps of the several races of mankind myself, but finding that Topinard ("L'Anthropologie," 1892) had already done so upon a very large series of skulls, and that my own observations, so far as they had been carried, were in complete accord with his, I desisted. Topinard, after rejecting all doubtful cases, includes in his record 595 human skulls, 120 anthropoid apes, and a very large number of lower apes.

He finds that M_1 was quadricuspid, with a well-marked oblique ridge in 99 per cent. of human skulls taken without distinction of race, so that

$\underline{M_1}$ is constant in all races.

$\underline{M_2}$ had 4 cusps in 66 per cent. of all races.
,, 3½ ,, ,, 16 ,, ,, ,, ,,
,, 3 ,, ,, 16 ,, ,, ,, ,,

(By 3½ is meant three well-developed cusps with an indication of the fourth.)

$\underline{M_2}$ has the normal four cusps in 79 per cent. of Malays, 83 of New Caledonians and New Hebrideans, 78 of Melanesians, 73 of Australians and Tasmanians; but the percentage falls to 58 in European, Semitic and Egyptian skulls, and to 68 in Chinese and Japanese.

$\underline{M_3}$ had 4 cusps in 37 per cent.
,, 3½ ,, ,, 11 ,, ,,
,, 3 ,, ,, 39 ,, ,,
,, 2 ,, ,, 5 ,, ,,

and was totally irregular in 6 per cent.

For lower molars he gives for all races,

$\overline{M_1}$, 5 cusps in 82 per cent.
4½ ,, ,, 4 ,, ,,
4 ,, ,, 10 ,, ,,

Thus $\overline{M_1}$ retains its type strongly, though less decidedly so than $\underline{M_1}$.

$\overline{M_2}$, 5 cusps in 24 per cent.
4½ ,, ,, 10 ,, ,,
4 ,, ,, 64 ,, ,,

$\overline{M_2}$, is distinctly a quadricuspid tooth, but less constantly than $\overline{M_1}$ is quinquicuspid.

$\overline{M_3}$, 5 cusps in 46 per cent.
4½ ,, ,, 6 ,, ,,
4 ,, ,, 31 ,, ,,

And $\overline{M_3}$ is very variable.

$\underline{M_3}$ had four cusps in 72 per cent. of Melanesians, 69 in Egyptian groups, and only 36 per cent. in European skulls.

It had three cusps in 56 per cent. of Chinese and in 47 per cent. of Negroes and Australians.

Thus, as he remarks, the third upper molars tend to be "disordered" in almost all races.

The race comparisons come out thus:—

In Europeans M_1 is getting away from its original type, which occurs in only 61 per cent. Polynesians have the full five cusps in 91 per cent.; Chinese and Japanese in 87 per cent.; Melanesians in 86 per cent.; Negroes in 88 per cent., and Egyptians in 77 per cent.

M_2 has the typical four cusps in Egyptians in 75 per cent.; in Europeans in 60 per cent.; in Negroes in 52 per cent.; in Polynesians in 52 per cent., and in Japanese in 44 per cent.; whilst it has five cusps in 33 per cent. of Melanesian skulls; in 30 per cent. of Malays, and in 37 per cent. of Chinese and Japanese.

From his observations he concludes that the teeth of man are in process of transformation, the lower molars tending towards a quadricuspid type with a crucial fissure, and the upper towards a tricuspid type.

In the former it is the fifth cusp which, from comparison with the teeth of apes, he holds to primarily originate in the middle line, in a bifurcation of the posterior arm of the cross, but to tend to displacement to the outer aspect of the crown more and more, till it disappears.

In the upper molars it is the postero-internal cusp which disappears, so that the tooth terminates backwards with the oblique ridge.

When it is further reduced to two cusps, it is by the fusion into one of the antero- and postero-external cusps: this manner of suppression of cusps brings the human tricuspid molar into close resemblance to the trituberculate lemurine tooth; but, as is set forth in the footnote below, he by no means agrees with Osborn in the determination of the homologies of the cusps severally (1).

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(1) Topinard holds that the antero-external cusp is the Protocone, *both in upper and lower molars*, therein differing from Osborn, and that the postero-external is the Metacone, the Paracone being absent in Primates,

It is held by Cope to indicate that the upper molars of European races show a tendency to revert towards the Eocene tritubereulate lemurine tooth.

The range of variation in the size of the jaws of healthy, otherwise well-developed adults is great: thus the smallest jaw (occurring in a man of stout build, above middle height) with which I am acquainted measures in width only 1½ inch, and in length from back to front 1¾ inch; while the largest (occurring in a gentleman of lesser stature; of Basque extraction, moreover, which makes it the more striking) (¹) measures no less than 2½ inches in width and 2¼ inches in length: and even larger dimensions are recorded in the "Dental Cosmos" of September, 1876; the width being taken between the centre of the alveolar borders at the position of the wisdom teeth, and the length being measured on a line drawn from the incisors to another line joining the two wisdom teeth.

On the whole, it must be said that there are fewer constant differences between the teeth of the various races of mankind than might have been *à priori* expected; in fact, we may almost say that the teeth of savage man are pretty much what we should look upon as an exceedingly perfectly formed set of teeth if we were to see them in the mouth of a European.

Professor Flower ("Journ. Anthropol. Instit.," March, 1885) has investigated the relation of the size of the teeth to that of the skull very closely, with the result of bringing out certain race distinctions. As measures for comparison he takes the length of the cranio-facial axis, measured from the front edge of the occipital foramen to the naso-frontal suture, and the length from the front of the first premolar

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and both the internal cusps being secondary acquisitions. He states that in both jaws in development the antero-external is the first to appear, and long keeps a preponderance, the antero-internal following, then the postero-external, and much later the postero-internal.

(¹) Magitot ("Bullet. de la Soc. Anthropol. de Paris," 1869) says:—"Les Basques, par exemple, remarquables par la petitesse extrême de leurs dents."

to the back of the third molar *in situ.* His "Dental Index" is arrived at thus:

$$\text{Dental Index} = \frac{\text{Length of Teeth} \times 100}{\text{Cranio-facial axis}}.$$

This gives figures ranging from 42 (microdont), 43 (mesodont), 44 and upwards (megadont).

As in the female the skull is smaller whilst the teeth are the same, a slightly higher index is arrived at in them:

The Microdont races are—

European.	Egyptian.
British.	Polynesian.

Or the Mesodont are—

Chinese.	Malays.
American Indian.	Negroes.

And the Megadont—

Melanesians.	Australian.
Andamanese.	Tasmanian.

As to this classification it is to be remarked that the teeth of Polynesians are actually larger than those of Europeans, but the cranio-facial axis is of extreme length, so that the index is reduced; this is also the case with the American Indians, whilst the Andamanese are brought into the Megadont series by the relative size of teeth to the basis cranii, though in this small people the teeth are actually small.

The dental index of Megadont races being from 44–47, that of the chimpanzee is little more than the highest of these, namely, 47·9, whilst the orang rises to 55, and the gorilla to 54, but in the gibbon the index is as low as 41·7. It is, however, the opinion of the African traveller, Mr. Stanley, that the teeth of African races vary in accordance with the build of the individual, and particularly with the size of the jaws, such small races as the Somalis having small teeth. It does not appear, however, that these impressions are based upon actual exact measurement, but only upon general appearance. He mentions that many of the races who show no regard for cleanliness otherwise, assiduously clean their teeth.

It now remains to describe the teeth of man in detail.

The teeth of the upper jaw are ranged along a curve of larger dimensions than those of the lower, the incisors passing in front of the corresponding lower teeth, and the external cusps of the bicuspids and molars closing outside those of the lower teeth.

There are, however, some points of detail to be noted in the relation borne by the upper to the lower teeth, besides that comprised in the general statement that the former lie outside the latter, by which it is brought about that each tooth is antagonised by portions of two teeth in the other jaw, and has therefore not merely a single opponent.

The upper incisors and canines, when the mouth is closed, from the larger size of the arch in which they are arranged, shut over and in front of the lower teeth, concealing the upper thirds of their crowns; while the external tubercles of the bicuspids and molars of the lower jaw are received into the depressions between the external and internal tubercules of the similar teeth in the upper jaw, thus allowing the external tubercles of the upper teeth to close externally to the outer tubercles of the lower row.

From this arrangement of the tubercles, we are enabled in mastication to use the whole surface of the crowns of the opposing teeth; the act of mastication being performed by bringing the external tubercles of the under molars opposite to those of the upper row; whence, by the lateral motion of the under jaw inwards, their external tubercles pass down the inclined surfaces of the external, and up those of the internal tubercles of the upper teeth, crushing in this action any interposed substance.

It will also be observed that, from the difference of width in the incisors of the two jaws, the central incisors of the upper extend over the centrals and half of the laterals of the under row, and that the superior laterals lie over the remaining half of the inferior laterals and the anterior half of the canines of the lower jaw. The upper canines close over the halves of the lower canines and first bicuspids, while the first bicuspids impinge on the half of the first and half of the second bicuspids of the lower row. The second upper bicuspids close upon the anterior third of the opposing lower first molars and the posterior halves of the second bicuspids.

The upper first molars oppose the posterior two-thirds of the first, and one-third of the second molars of the lower jaw, while the second upper molars close upon the unoccupied posterior third of the second and the anterior third of the wisdom teeth. The wisdom tooth of the upper being smaller in size than that of the lower jaw is perfectly opposed by that portion of the latter left unoccupied by the second under molar tooth.

By this admirable arrangement no two teeth oppose each other only, but each tooth in closure of the jaw impinges upon two, so that should a tooth be lost, or even two alternate teeth, still the corresponding teeth of the opposite jaw are to some extent opposed, and thus remain useful. For when a tooth is wholly unopposed, a process is apt to be set up in the jaw by which the useless organ is gradually ejected. The direction of the teeth in the upper is vertically downwards and slightly forwards, while those of the lower jaw are placed vertically, the molars tending slightly inwards.

The fantastic theory of Dr. Bonwill, that the form of the jaws and teeth is referable to developments of a triangle, a theory which he holds to upset the whole doctrine of evolution, does not call for serious discussion; and it would not have been mentioned at all here had it not been unaccountably admitted into the last American edition of "Gray's Anatomy."

For the purpose of description three parts of the tooth are distinguished by name, viz., the crown, neck, and root.

This distinction of parts which we make in describing human teeth, when we speak of crown, neck, and root, is applicable to the great majority of mammalian teeth, though there are some few forms of teeth in which no such differentiation of parts can be seen.

The crown is that portion which is exposed above the borders of the gum, and is in human teeth coated with enamel; the neck is that portion which corresponds to the edge of the gum, and intervenes between the edges of the bony sockets and the edge of the enamel; the root is that part which is enclosed within the bony socket, and is covered by cementum.

Of these it is to be remarked that the "neck," although a convenient and necessary term for descriptive purposes, marks an arbitrary division of less importance than that expressed by crown and root; also that although this division into three parts can be made in the case of socketed teeth of limited growth, no such distinction of parts can be made in teeth of perpetual growth.

Special names have been applied to the various surfaces of the crowns, as, owing to the curvature of the alveolar border, terms which have references to back, front, or sides would in different parts of the mouth, indicate different surfaces, and so lead to confusion.

The lips and tongue and the median line of the mouth, however, are not open to this objection, so the surfaces which are directed outwards towards the lips are called "labial;" and those inwards towards the tongue "lingual;" the interstitial surfaces are called "median" and "distal."

In viewing the gradational characters which exist between the various human teeth, it must not be forgotten that some links in the chain have dropped out and are absent. Mention has already been made of the full typical number of mammalian teeth being 44, *i.e.*,

$$\text{I. } \frac{3}{3} \text{ c } \frac{1}{1} \text{ prm. } \frac{4}{4} \text{ m. } \frac{3}{3} = 44;$$

whereas man has only

$$\text{i } \frac{2}{2} \text{ c } \frac{1}{1} \text{ pm } \frac{2}{2} \text{ m } \frac{3}{3} = 32.$$

It has been usual to suppose that the teeth which are missing in man are the third incisor on each side and the first and second premolars, but reasons have been advanced which throw doubt upon this conclusion as regards the incisors. (Albrecht, "Zoolog. Anzeig.," 1879; Professor Sir W. Turner, "J. Anat. and Phys.," 1885; A. Wilson, "British Dental Association Journal," April, 1885; Edwards, *idem*, December, 1885; Windle and Humphreys, "J. Anat. and Phys.," Vol. XXI.) From the study of cases of cleft palate it has been found that it is not at all certain that the cleft usually runs along the site of the suture between the intermaxillary bones and the maxilla, for it often appears to be well within the limits of the intermaxillary bone, and so lends some support to the idea of Albrecht that there are two intermaxillary bones on each side (1), and that the cleft runs along the division between them. And it is far from uncommon for a tooth of incisor type to lie beyond the cleft and close against the front of the canine; to this tooth Sir W. Turner, pending decision as to its homologies, gives the name of precanine. The argument put briefly is this; a tooth outside the cleft and close to the canine is so common of occurrence that its position there must be due to something other than accident, the normal number of incisors not being exceeded. But there is a case on record in which this precanine existed although there were four incisors upon the intermaxillary portion, which was isolated by a double cleft; in this specimen, therefore, the precanine was evidently i^3 of the normal mammalian dentition, and it is therefore not unlikely that it is always so; if this inference be correct, then the lost incisor in man is probably i^2.

Incisors.—Of these there are four in each jaw; two central, two lateral incisors. Their working surfaces form wedges, or obtuse and blunt-edged chisels, calculated to divide food of moderate consistency.

Upper Incisors.—The centrals are very much larger than the laterals, and viewed either from the back or front taper with some regularity from the cutting edge to the point of the root, the neck not being marked by strong constriction. The crown of the tooth, as seen from the front, is squarish, or more strictly, oblong, its length being greater than its breadth.

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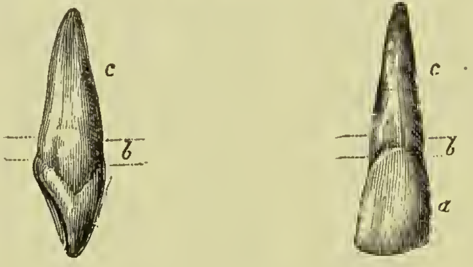
(1) Comparative anatomy, however, lends no support to this view.

The median side, by which it is in contact with its fellow, is a little longer than the distal, so that the median angle of the crown is a little lower, and, as a necessary consequence, a little more acute than the distal angle of the cutting edge. Near to its base the crowns narrow rather abruptly, so that near to the neck a space is left between the contiguous teeth.

The labial surface is slightly convex in each direction, and often presents two slight longitudinal depressions, which end at the cutting edge in slight notches, though in well-formed typical teeth these grooves are not distinguishable.

Fig. 248 ([1]).



In recently-cut teeth the thin cutting edge is elevated into three slight cusps, which soon wear down and disappear after the tooth has been in use.

The edge of an incisor may be regarded as formed by the bevelling off of the dentine of the lingual surface, which is nearly flat from side to side, with a slight tendency to concavity, while from above downwards it is distinctly concave, and often presents longitudinal depressions similar to those on the labial surface. The lingual surface towards the gum terminates in a distinct prominence, oftentimes amounting to a bounding ring of enamel, termed the *basal ridge*, or, in the language of comparative anatomy, the *cingulum*. It is variable in the extent of its development; it rarely rises into a central prominence at the back, but in the angle

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([1]) Front and side view of a left upper central incisor. *a.* Distal surface. *b.* Neck. *c.* Root.

where the ridges of the two sides meet a deep pit is sometimes left in the enamel, though this must be regarded as a departure from the normal; this is a favourite site for caries. The crown, or what amounts to the same thing, the enamel, terminates on the lingual and labial aspect of the tooth in a curved line, the convexity of the curve being directed upwards towards the gum; on the interstitial surfaces, both median and distal, the curve is less regular, and its contour would be more correctly described as V-shaped, the apex of the V being towards the crown of the tooth and away from the gum. The dentist will do well to remember the disposition of the enamel in this situation, as it is a point of some importance in shaping the cervical edge of a cavity preparatory to filling it.

The transverse indentations of the enamel met with both on lingual and labial surfaces, though more especially in the latter, are marks of arrest of development, and, common as they are, are to be regarded as abnormalities.

The central incisors are larger than the laterals, though not in so great degree as is the case in the anthropoid apes.

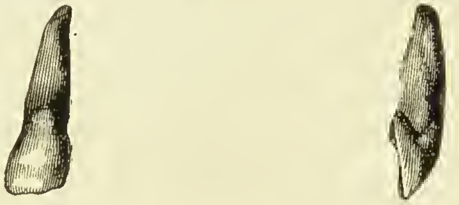
The pulp cavity bears a general resemblance to the external contour of the tooth; towards the cutting edge it is very thin, and is prolonged to its two corners to a slight extent into "cornua;" at the neck it is cylindrical, and is also cylindrical in the root, tapering gradually till it approaches close to the apex, when it becomes suddenly constricted.

Upper Lateral Incisors are in every dimension somewhat smaller than the centrals. They widen somewhat abruptly near to the cutting edge, but below this they taper pretty regularly to the end of the root; the labial surface is convex in each direction, while the lingual surface is perhaps rather flatter than that of a central incisor.

The outer (distal) angle of the crown is far more rounded or sloped away than in the centrals, and the distal surface, looking towards the canine, is in a slight degree convex; the median surface may be slightly concave.

The enamel terminates towards the gum in contours precisely similar to those which obtain in the centrals: but the basal ridge, or cingulum, is often more strongly pronounced, and the presence of a central tubercle upon it is less infrequent. From this greater prominence of the cingulum and consequent more marked depression in front of it, caries is more frequent upon the lingual surfaces of upper lateral than upon those of upper central incisors.

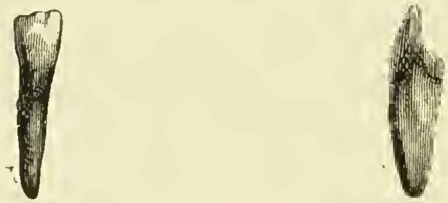
Fig. 249 (1).



The pulp cavity is, relatively to the whole tooth, perhaps a little larger than in the central incisors; in other respects the same description will suffice.

Lower Central Incisors are very much narrower than those of the upper jaw; not more than half the width at their cutting edges, which again are much wider than the necks of the teeth.

Fig. 250 (2).



From before backwards they are deep at the neck; hence the roots are very much flattened from side to side, and rotation is inadmissible in the attempt to extract them.

The enamel contour at the neck is similar to that of the upper incisors, but there is no well-marked cingulum.

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(1) Front and side view of a left upper lateral incisor.

(2) Front and side view of lower central incisor.

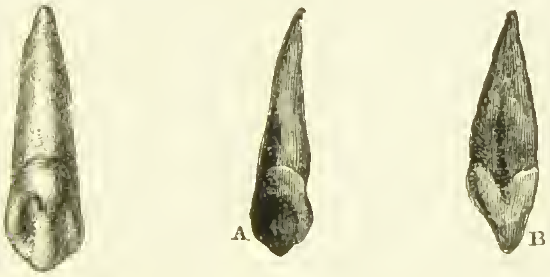
Lower Lateral Incisors are, unlike the upper teeth, distinctly larger than the centrals in each one of their dimensions, but more especially in the length of their roots, which are much flattened, and often present on their sides a median longitudinal depression, sometimes amounting to an actual groove.

The distal angle of the crown is rounded off like that of the upper lateral incisors, though not so markedly.

Canines, Cuspidati, Eye Teeth, are in all respects stouter teeth than the incisors; not only are the crowns thicker and stronger, but the roots are very much longer.

The crown terminates in a blunt point, which lies in a straight line with the long axis of the root; a feebly pronounced line or ridge runs down the outer surface of the tooth from this point to the neck. The crown slopes away both before and behind the point or cusp, but as that side of the tooth which lies next to the bicuspid is convex, and as it were produced towards that tooth, the slope is longer on the distal than on the mesial half of the crown. The crown thus not being perfectly symmetrical renders it easy to determine at a glance to which side of the mouth the canine belongs.

Fig. 251 ([1]).



The internal or lingual surface is not concave like that of the incisors, but is in a slight degree convex, and a median ridge runs down it from the apex of the cusp; this ridge where it meets with the ridge which borders the lingual surface and corresponds with the cingulum of the incisor teeth, is often developed into a well-marked prominence or cusp.

([1]) Lingual, labial, and distal surfaces of an upper canine, showing the basal cusp and the three ridges which converge towards it.

In transverse section the neck is somewhat triangular, with the angles rounded, the outer or labial being much wider than the lingual aspect.

Lower canines are less pronounced in form than the corresponding upper teeth; the point is more blunted, the root shorter, the perpendicular labial ridge not traceable, and the want of symmetry between the mesial and distal halves of the crown less marked. The lingual surface has perhaps a greater tendency to concavity.

Premolars, Bicuspids, are eight in number, two on each side of both upper and lower jaws, and they correspond to the third and fourth premolars of the typical mammalian dentition, the first and second premolars not being represented in man ([1]).

Upper Premolars.—The crown, as seen looking upon its grinding surface, is roughly quadrilateral, its outer or labial border being, however, larger and thicker than its inner, and the teeth are carried round the curve of the alveolar border mainly by means of this difference in size in the external and internal portions of the canines and the two bicuspids.

As is implied by its name, the crown has two cusps, of which the outer is the larger, stouter, and broader. The outer and inner surfaces (labial and lingual) are convex and smooth, with no basal ridges at the edge of the gums. It is, however, not uncommon, especially in the lower races of mankind, to see some indication of a median ridge upon the labial surface, defined by slight grooves upon either side.

The inner and outer cusps are not joined by a ridge; instead of this there is a deep transverse fissure, the ends of which turn somewhat abruptly outwards towards the labial aspect of the tooth; perhaps the cingulum has been elevated to form the inner cusp, and forms slight elevations bordering the anterior and posterior (median and distal) edges of the grinding surface. The median surface, where it fits against the canine, is concave.

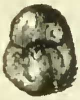
The root is single, and much compressed from side to

([1]) Mr. A. Wilson holds that pm. 1 and pm. 4 have disappeared.

side: very often, however, it is double for the greater part of its length, and if not so divided is often marked by a groove upon each side indicating a tendency towards such division. The outer border of the root is also often marked by a longitudinal furrow, which may amount to complete division. The tendency to division is so frequent both in lower and higher races that it may be regarded as almost normal. In fact, a bicuspid may have three perfectly distinct roots, like a molar, and like the premolars of monkeys, in which three is the normal number of roots. The first bicuspid is more variable in respect of its roots than the second.

It is thought by Topinard that in the passage from a three-rooted to a single-rooted type the postero-external root is lost, the antero-external and internal roots becoming fused.

FIG. 252 (¹).



The second upper bicuspid differs from the first in that the difference in size between its outer and inner cusps is less, the inner cusp being relatively considerably larger, and indeed often preponderating over the labial cusp in length, so that the labial and lingual surfaces are nearly equal.

The pulp cavity in the crown is furnished with distinct cornua; at the neck it is very much flattened from side to side, being often reduced to a mere fissure, which is, however, considerably larger at its two extremities than in its middle. Hence the pulp cavity of an upper bicuspid is difficult to fill; a difficulty again increased by the impossibility of always discovering what number of fangs it has, as their division sometimes takes place rather high up.

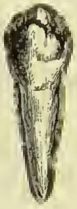
Lower Premolars are smaller teeth than those of the

(¹) Grinding surface of an upper bicuspid.

upper jaw, and are quite distinct in shape. The outer or labial cusp is bent inwards, and the labial surface of the crown is very convex. The inner cusp is very feebly developed, and is connected with the outer by a low ridge ; it is also narrow, so that the tooth is triangular as looked upon from above.

The root is rounded, a little larger on its outer side than on its inner, and tapers regularly towards its point; the pulp cavity is cylindrical at the neck, and also tapers regularly in the root. The cornu of the pulp which corresponds to the inner cusp, is feebly developed.

FIG. 253 (1).



The second lower bicuspid differs a good deal from the first ; its crown is much squarer and larger in all its dimensions. The inner cusp reaches to a higher level and is stouter, and the greater development of the ridges which bound the anterior and posterior borders of the grinding surface makes it attain to such a large size as to make the tendency towards a transition from the bicuspid type to that of a true molar very evident.

Having completed the brief description of the forms of these several teeth, it is worth while to note one or two general characters of the series. The differences between a well-marked incisor, canine, or premolar are so strongly pronounced that the resemblances which underlie them are apt to be overlooked, and it might be supposed that in shape they had little in common.

Nevertheless a very distinct gradation may be traced, and it is far from uncommon to meet with teeth which possess in a marked degree transitional characters. If the external or distal angle of a lateral incisor be sloped off more than usual, while at the same time its cingulum and basal prominence be well marked, it makes no bad imitation of a diminutive canine; and such laterals are often to be met with by any who search for such deviations from the normal form.

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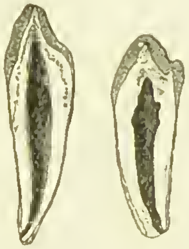
(1) Lower first bicuspid, seen from the inner side, and showing the preponderance of its outer over its inner cusp.

Thus the form characteristic of a lateral incisor, if it be a little exaggerated, very nearly gives us the form of a canine; indeed, if we look at the teeth of an orang the lateral incisor is to all intents a diminutive canine; and in the present discussion the great comparative size of the canine, which is traceable to readily intelligible causes, may be put aside, as it tends to obscure the point to be here insisted on.

FIG. 254 (¹).



Between the canines and the bicuspids a similar relationship in form exists, and it is more apparent in the lower than in the upper jaw. The fact that at the base of the inner or lingual aspect of the canine may be found an elevation of the cingulum, in many instances amounting to a low cusp, has been already noted; and it has been already pointed out that the inner cusp of the first lower bicuspid is both smaller and lower than the other, indeed often can hardly be said to exist. A longitudinal section through the crowns of the two teeth will demonstrate without the necessity of further description that the basal cusp of the canine and the

---

(¹) Section of a lower canine and first bicuspid, showing the characters common to the two.

inner cusp of the bicuspid are the same thing, differing only in degree, while it is interesting to note that the pulp chamber in the bicuspid has hardly any prolongation towards the small inner cusp, so that the resemblance between the two teeth is thus made more complete.

This close relationship of canines and bicuspids has been considered in the chapter on the Homologies of the Teeth; for our present purpose it will suffice to merely point out its existence. The transition from the bicuspids to the molars is more abrupt; at least it is not so easy to point out exactly how a modification of the one would arrive at the form of the other. But it merely needs an exaggeration of the differences existing between a canine and a first bicuspid to make a good imitation of a second bicuspid.

If any one will take the trouble to make mental note of the deviations in form which he meets with in teeth, he will find that they almost invariably consist of approaches towards the form of the teeth on either side of them; and will infallibly be led to the conclusion that incisors, canines, and bicuspids are not three patterns of teeth perfectly distinct, and each *sui generis*, but that they are modifications of one and the same pattern. I may add, that comparative odontology teaches us the same thing, and demonstrates clearly the substantial identity of origin of the three forms, as also of the true molars.

Upper Molar teeth have crowns of squarish form, the angles being much rounded off. It may be premised that the first molar is more constant in shape than the second (it was regular in 99 per cent. of skulls examined), and this latter than the third; with this proviso the first and second may be described together.

The masticating surface carries four sub-equal cusps, two labial or external and two lingual or internal; the anterior internal cusp is distinctly the largest, and it is connected with the posterior external cusp by a thick oblique ridge of enamel, the remaining two cusps having no such connection.

This oblique ridge on the upper molars is met with in man, the anthropoid apes, and certain new-world monkeys.

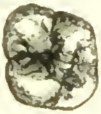
The identification of the cusps as propounded by Professor Osborn is as follows :—

Antero-internal = Protocone }
Antero-external = Paracone } Primitive triangle or trigon.
Postero-external = Metacone }
Postero-internal = Hypocone : Primitive heel or talon.

Topinard, however, interprets these differently. (See p. 524.)

The grooves which separate the cusps pass down on to the labial and lingual surfaces of the crown, but are lost before reaching the gum ; where they terminate, however, there is often a pit, which is a very favourite situation for caries, especially on the labial aspect of the teeth. It is very rare to see the grooves passing down upon the mesial or distal surfaces of the crown, a raised border of enamel generally cutting them short in this direction.

Fig. 255 (1).



When one cusp is suppressed, it is always the postero-internal, the tooth then ending with the oblique ridge.

The roots are three in number, two external or labial, and one internal or palatal. The latter is the largest, and runs in a direction more strongly divergent from the axis of the crown than the other roots. It is directed obliquely inwards towards the roof of the palate, is sub-cylindrical, and often curved.

The external roots are less cylindrical, being mutually compressed, so that their largest diameter is transverse to the dental arch ; the anterior is rather the larger of the two, and is more strongly pronounced on the side of the neck of the root. The anterior labial root is occasionally confluent with the palatine root, but still more frequently the posterior labial and palatine roots are confluent: occasionally, also, four distinct roots may be met with.

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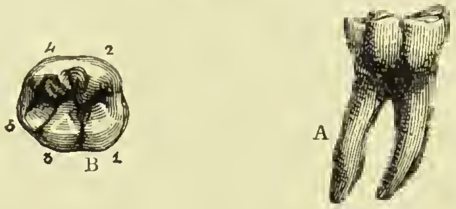
(1) Masticating surface of a first upper molar of the left side ; the oblique ridge connects the anterior internal with the posterior external cusp.

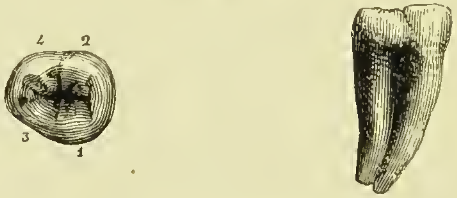
Third Molars, *dentes sapientiæ*, wisdom teeth, of the upper jaw, resemble in a general way the first and second molars, that is, when they are well developed and placed in a roomy dental arch. But amongst most civilised races it may almost be said to be exceptional for the wisdom teeth to be regular either in form or position, so that extreme variability prevails among these teeth.

Fig. 256 (1).



The two inner tubercles are often blended together and the roots confluent, forming an abruptly tapering cone, the apex of which is often bent and crooked, so that but little vestige of the three roots can be traced, the pulp cavity even being quite single.

Fig. 257 (2).



Lower Molars.—The first lower molar is the most constant in form, and is somewhat the largest; its grinding surface presents five cusps.

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(1) Masticating surface of a first lower molar, right side, the five cusps of which are indicated by figures.

(2) Second lower molar of right side, the four cusps being indicated by figures. The tooth figured is not so square as it should be, its posterior cusps as well as its posterior root being smaller than the normal.

Four cusps are placed regularly at the four corners of a square, these being divided from one another by a crucial fissure; the posterior arm of the crucial fissure bifurcates, and between its diverging arms is the fifth cusp, which may occupy the median line, but more often is somewhat to the outer side; it is distinctly visible when viewed from the labial aspect. According to Osborn, the homologies of the cusps are as follows:—

Antero-external = Protoconid ⎫ Two cusps of the primitive
Antero-internal = Metaconid ⎭ triangle.
Postero-external = Hypoconid ⎫
Postero-internal = Entoconid ⎬ Primitive heel.
Postero-mesial = Hypoconulid ⎭

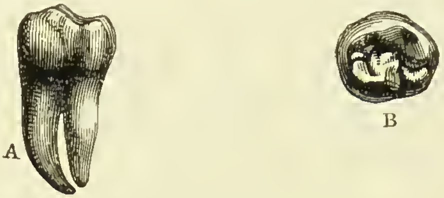
The transverse fissure passes over the limits of the grinding surface, and on the outside or labial surface of the tooth may end in a pit, which is a common site for caries; although it occasionally passes over the lingual surface, it is here less pronounced. They are implanted by two roots, placed anteriorly and posteriorly; the roots are much flattened from before backwards, and they are very usually curved slightly backwards. In the median line of each root there is usually a groove, by the deepening of which four roots may be produced; or this may happen with the one root only, so that a three-rooted tooth is the result. The first lower molar has five cusps in 82 per cent. of all skulls examined.

The second molar does not greatly differ from the first save that the roots are more often confluent, and the fifth cusp less marked, even if it exists at all. It is present in about 24 per cent. of skulls.

Third Lower Molar.—This tooth is seldom so small as the corresponding upper tooth, and its crown is often large even when its roots are very stunted. It has five cusps as a rule, and bears a more or less close resemblance to the molars which precede it. It is either two-rooted, or if the roots be confluent, a groove usually marks a tendency to divisions into two fangs.

It is stated by Professor Owen ("Odontography," p. 454) that although the wisdom tooth is the smallest of the three molars, the difference is less marked in the Melanesian than in the Caucasian races, adding also that the triple implantation of the upper and the double implantation of the lower is constant in the former races. More extended observations have overthrown this statement as a positive dictum to be accepted without exceptions, but it may nevertheless be taken as expressing a general truth.

Fig. 258 (1).



In lower molars the inner, and in the upper the outer cusps are longer.

The milk teeth differ from the permanent teeth by being smaller, and having the enamel terminating at the neck with a thick edge, so that the neck is more strongly constricted. The incisors and canines are somewhat similar to their successors, the canines, however, being relatively shorter and broader than their successors. The first upper molars have three cusps, two external and one internal : the second more nearly resemble the permanent molars.

The second lower deciduous molar has four cusps and resembles a second lower permanent molar. The roots of the deciduous teeth diverge from the neck at greater angles than those of permanent teeth, in consequence of their more or less completely enclosing between them the crypts in which the latter are developing.

(1) Third lower molar of the left side.

CHAPTER XV.

THE MAXILLARY BONES.

The teeth are implanted in bone specially developed for the purpose; they lie at the period of their eruption in a wide excavation in the bone in which they are free to move under the influence of very slight forces, and the bone in which they are held was moulded around their roots subsequently to their being formed and moved into position.

The manner of attachment of the human teeth is that termed "gomphosis," *i.e.*, an attachment comparable to the fitting of a peg into a hole: the bony sockets, however, allow of a considerable degree of motion, as may be seen by examining the teeth in a dry skull, the fitting being in the fresh state completed by the interposition of the dense periosteum of the socket. This latter, by its elasticity, allows of a small degree of motion in the tooth, and so doubtless diminishes the shock which would be occasioned by mastication were the teeth perfectly immovable and without a yielding lining within their bony sockets. When this becomes inflamed and swollen by exudation the tooth is pushed to a certain degree out of the socket, and so being to a less extent limited in its range by the bony socket, acquires an increased mobility.

The teeth are in all mammalia confined to the bones which carry them in man, namely, the intermaxillary and maxillary bones and the lower maxillary bone or mandible.

As full descriptions of these bones (1) will be found in any general anatomical work, only points in their anatomy which directly concern the dental student will be mentioned here.

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(1) Much that is of great interest, and that is not to be found in text books, is embodied in a series of papers on "The Facial Region," by Dr. Harrison Allen ("American Dental Cosmos," 1873-74).

The alveolar process is a strong wide ridge of bone, curved so as to form with that of the other maxillary bone the elliptical figure characteristic of the dental arch in the higher races. It may be described as consisting of two plates, an outer and an inner, which are connected by numerous transverse septa, the sockets of the teeth being formed by the interspaces between these septa. The internal alveolar plate is the stronger, the external the thinner and weaker, a fact of which we take advantage when we extract a tooth by bending it slightly outwards. On the outer surface of the alveolar process are eminences corresponding to the roots of the teeth, and depressions in their interspaces, apt to be especially marked over the canine teeth ; while between the teeth the alveolar processes attain to a lower level, so that the margins of the bone are festooned. Looking down into an empty socket, the bone is seen to be everywhere very porous, and to be perforated by foramina of considerable size, while at the bottom there is the larger foramen admitting the vessels and nerves of the tooth.

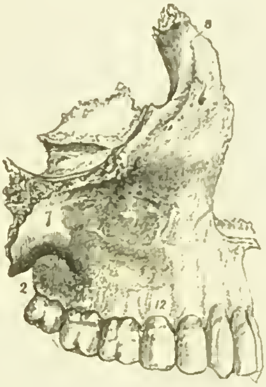
The alveolus of each individual tooth consists of a shell of comparatively dense bone of small thickness, which is imbedded in a mass of loose spongy bone; this dense shell comes into relation with the dense cortical bone of the jaw mainly at its free margin, near to the neck of the tooth. Over very prominent roots a portion of alveolus is at times wanting, so that in a macerated skull the root is exposed to view.

This difference between the bone constituting the immediate alveoli and that constituting the shell of the jaw bones is very strongly marked in some mammals, notably in the manatee, in which there appears to be a continual migration of teeth forwards taking place during the animal's life. (See p. 388.)

The upper maxilla serves to give form and support to the soft parts of the face, and also to carry the upper teeth.

These have to be rigidly fixed, while the teeth of the lower jaw are brought forcibly against them with more or less of shock. And whilst these blows have to be received, and resisted, and ultimately borne by the cranium, it is obviously desirable that they should be distributed over a sufficiently wide area, so as not to be felt unpleasantly.

FIG. 259 (1).



The ascending nasal process is very stout, and serves to connect the maxilla strongly with the frontal bone, which also in the region in question is powerfully developed; the thick malar process gives rigidity and resistance to lateral movements of the jaws, and carries off the strains to the lateral walls of the cranium; the maxilla is buttressed at the back by the pterygoid processes.

Taking next the various surfaces of the bone, there are four, or, if we include the palatine aspect, five: the external, forming a large part of the face, the superior or orbital, the internal or nasal, and the posterior or zygomatic. Upon the external or facial surface we have to note the eminence caused by the socket of the canine tooth ("canine eminence"), and immediately behind this a depression, the canine fossa, through which the antrum is sometimes punctured. The alveolar border, from the situation of the

(1) Superior maxillary bone of right side. 1. Body. 2. Tuberosity. 7. Malar process. 8. Nasal process. 12. Alveolar process.

third molar to that of the second bicuspid, gives attachment to the buccinator muscle; while immediately beneath the margin of the orbit is the infra-orbital foramen, whence issues the infra-orbital nerve; hence this is one of the situations to which neuralgic pain really dependent on the teeth may be referred.

The orbital and nasal surfaces concern us only through their relation to the antrum, to be presently described; in the zygomatic surface, which is convex and forms part of the zygomatic fossa, are several orifices transmitting the posterior dental nerves and vessels; a groove which, converted by the apposition of the palate bone into a canal, forms the posterior palatine canal; and at the bottom, a rounded eminence, the maxillary tuberosity, which lies behind the wisdom tooth, and has been occasionally broken off in extracting that tooth.

The body of the bone is excavated by an air-chamber, the antrum, which is coated in life by a continuation of the nasal mucous membrane, and this frequently becomes secondarily involved in dental disease, so that its anatomical relations are of great importance to the dentist.

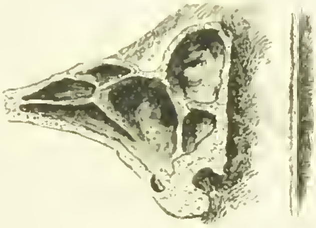
Like the somewhat similar air cavities in the frontal bone, the maxillary sinus does not attain to its full size, relatively to the rest of the bone, until after the age of puberty, although it makes its appearance earlier than the other nasal sinuses, its presence being demonstrable about the fifth month of fœtal life. Hence it follows that its walls are thicker in the young subject than in the adult; and, according to the observations of the late Mr. Cattlin (1), it is somewhat larger in the male than in the female.

It is very variable in size, so that out of one hundred adult specimens the above-mentioned writer found one which would only contain one drachm of fluid, while in contrast with that was another which held eight drachms; two and a half drachms being the average capacity. Although it is exceedingly variable in form as well as in size, it tends

(1) "Transactions of the Odontological Society," Vol. II., 1857.

towards a roughly pyramidal shape, the apex of the pyramid being directed towards the malar bone, which it has been seen to encroach upon, and the base towards the nasal cavity; it is, however, useless to minutely describe its form, inasmuch as the two antra in the same individual are sometimes quite dissimilar. The floor of the cavity is rendered uneven in most specimens by prominences corresponding to the roots of the molar teeth, which ordinarily are but thinly covered by its bony walls, while it is not by any means rare to find some of them actually bare.

Fig. 260 (¹).



The cavity is also more or less completely subdivided by bony partitions springing from its walls, as is well exemplified in the accompanying figure; these partitions are for the most part thin, but they occasionally attain to considerable thickness, and they are stated to occur most frequently at the anterior or posterior angles of the base of the pyramid.

On the base of the pyramid is the orifice by which it opens into the middle meatus of the nose, this orifice being partly closed in by the ethmoid, palate, and inferior turbinated bones, and also by soft parts, so that in a recent subject it will barely admit a goosequill; and it should be noted that this orifice opens into the antrum near the top, so that it does not afford a ready means of egress to fluids accumulated in the cavity.

Through this orifice the mucous membrane lining the antrum is continuous with that of the nasal fossæ, and, like

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(¹) Section of an antrum of the left side, divided into many pouches by bony septa, and extending into the malar bone. Drawn from a specimen in the collection of Dr. Maynard, in the possession of the Baltimore Dental College.

that, it is ciliated; but it differs from it in being thinner and less vascular.

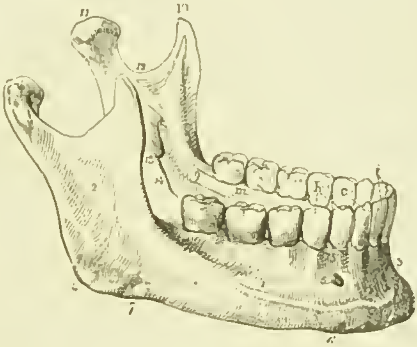
The canal which comes down from the frontal sinus opens very close to the antral foramen, there being often also a fold of mucous membrane in this position.

The teeth which usually come into the closest relation with the antrum are the first and second molars, but any of the teeth situated in the maxillary bone may encroach upon its walls, and I have more than once seen an abscess, originating at the apex of the root of a lateral incisor, pass backwards and perforate the antrum.

Its walls have four aspects, namely, towards the orbit, the nose, the zygomatic fossa, and the face, while its floor is formed by the alveolar border. With the exception only of the latter, its walls are very thin; and this exception has an important practical bearing in the diagnosis of tumours in this region, as accumulations of fluid or morbid growths really situated in the antrum bulge any or all of its walls in preference to the alveolar border, whereas tumours springing from the base of the sphenoid or elsewhere and encroaching upon the antrum, push down and distort the alveolar border as easily as any of the other walls of the cavity, inasmuch as the pressure caused by them is not transmitted equally in all directions, as is the case when the medium transmitting the power is a fluid.

The Lower Maxilla or mandible consists of a body and two rami, which ascend almost perpendicularly from its posterior extremity. The horizontal portion or body is curved somewhat in a parabolic form; it has a convex external and concave internal surface, and an upper (alveolar) and a lower border. On the convex facial surface we have to note the ridge marking the position of the symphysis, and below this the mental prominence, which is absent in anthropoid apes and also in some palæolithic men. Externally to this, below the line of contact of the first and second bicuspids (or a little below or behind this point) is the mental foramen, which constitutes the termination of the inferior dental canal. Running obliquely upwards, and first visible at a point a little distance from the mental prominence is the external oblique line, which becomes merged in the base of the coronoid process. Where it rises as high as the alveolar border, *i.e.*, opposite to the third and sometimes the second molar, the outer alveolar plate is strengthened by it, so that it becomes less yielding than the inner plate. The student should bear this fact in mind when extracting a lower wisdom tooth.

Fig. 261 (1).



The buccinator is attached to the alveolar border opposite to the molar teeth; the platysma myoides to the outer side of the lower border along a region somewhat further forward: the masseter over the whole outer face and border of the ascending ramus, and the temporal to the apex and side of the coronoid process. The other muscles attached to it are facial muscles of expression.

On the inner surface of the body are four tubercles, situated in pairs in the median line, about opposite to the ends of the roots of the incisors, but somewhat variable both in position and in size in different individuals. The upper pair of tubercles give attachment to the genio-hyo-glossus, the lower to the genio-hyoid muscles; they are interesting to the dental student not only as giving attachment to muscles concerned in deglutition, but as affording convenient fixed points for measurements of the relative growth of parts of the jaw. Beneath these genioid tubercles lie the slight depressions which give attachment to the anterior belly of the digastric muscle, while between the two points alluded to commences the internal oblique line, which runs obliquely upwards and backwards, becoming more pronounced as it extends backwards, and terminating at the inferior dental foramen. This internal oblique ridge marks the line of growth of the condyle (see Development of the Jaws), and gives attachment to the mylo-hyoid muscle, which forms the floor of the mouth, in all its length. Thus the bone above the ridge belongs strictly to the mouth, that below it has more relation with cervical structures. The depression for the sublingual gland is above this line, consequently this gland is visible from the mouth; that for the submaxillary gland is beneath it and further back.

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(1) Lower maxillary bone. 2. Ramus, where masseter is attached. 3. Symphysis. 5. Mental foramen. 6. External oblique line. 8. Angle of jaw. 9. Internal oblique line. 10. Coronoid process. 11. Condyle. 12. Sigmoid notch. 13. Inferior dental foramen.

The surface of the ascending ramus gives attachment to the following muscles: at the neck of the condyle to the external pterygoid; on the inner face of the coronoid process, as far down as the level of the top of the crown of the wisdom tooth, to the temporal; on the inner side of the angle, over a large surface, to the internal pterygoid.

The orifice of the inferior dental canal is rough and spinous, giving attachment to the internal lateral ligament of the jaw, while beneath and behind it is the groove for the mylo-hyoid vessels and nerves; the canal runs forward in the bone, a little distance beneath the ends of the roots of the teeth, and emerges at the mental foramen, turning outwards at an angle to reach it, and sending onwards small canals to the incisors, not traceable far. It is nearer to the outer than to the inner surface of the jaw in the latter half of its course, and is apt to be very close to the ends of the roots of the wisdom teeth, and to those of the bicuspids. The alveolar processes of the lower jaw, at their posterior part, diverge more widely than those of the upper jaw, the relative antagonism between the upper and lower teeth being preserved in this region by the former having an inclination outwards, the latter inwards. The ascending rami join the body at an angle which is very obtuse in the fœtus, nearly a right angle in the adult, and once again obtuse in advanced old age; the explanation of this change has been given under the head of the Development of the Jaw.

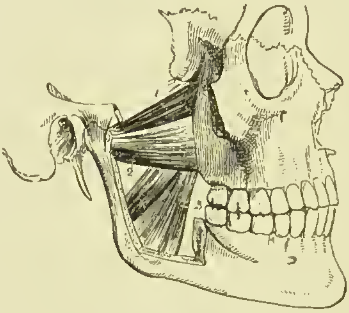
The articulation of the human lower jaw is peculiar, and allows of a degree of play unusual in a joint. The ovoid condyles, when the jaw is at rest, are lodged in depressions, the *glenoid fossæ* of the temporal bone, formed partly by the squamous and partly by the vaginal portions of the bone. The posterior half of the cavity is rough, and lodges a portion of the parotid gland: the anterior is smooth, and is bounded in front by the *eminentia articularis*, which is the middle root of the zygoma, enters into the formation of the joint, and is coated over by cartilage. Between the condyle of the lower jaw and the temporal bone lies a movable *inter-articular fibro-cartilage*, which is an irregular bi-concave oval plate, the edges of which are united with the capsular ligament, so that the joint is divided into two cavities, furnished with separate synovial membranes (unless when, as sometimes is the case, the fibro-cartilage is perforated in its centre).

The joint is described as having four ligaments: the capsular, stylo-maxillary, internal and external lateral ligaments.

The capsular ligament is but feebly pronounced, and hardly deserves the name; the stylo-maxillary reaches from the apex of the styloid process to the angle of the jaw; the internal lateral from the spine of the sphenoid to the margins of the inferior dental foramen; the external lateral, which alone is a ligament strictly proper to the articulation, reaches from the outer side and tubercle of the zygoma to the outer surface of the neck of the condyle.

The form of the articulating surfaces and the comparative absence of retaining ligaments combine to allow of a variety of movement unusual in any other than a ball-and-socket joint. The articulation acts as a simple hinge when the jaw is simply depressed, and this is the only motion possible in many animals, as in typical carnivora. When, however, the mouth is opened to the fullest possible extent, the condyle leaves the glenoid cavity, slides forward, and rests on the articular eminence, the interarticular fibro-cartilage being carried forward with it. The passage of the condyle on to the articular eminence, although always taking place when the lower jaw is excessively depressed, takes place sometimes with but little depression of the lower jaw, which then passes horizontally forward; or it may take place on the one side only, giving to the jaw the lateral movement so useful in mastication. In the mastication of food the various movements are combined, or succeed one another with great rapidity; the lateral movements are not very extensive, the outer cusps of the lower teeth of one side being brought to antagonise the outer cusps of the upper teeth, and then being made to slide forcibly down the sloping surfaces of the latter till they return to their normal antagonism; when one set of muscles is tired the same process is gone through on the other side of the mouth.

Fig. 262 (1).



The closure of the jaw, and the rotatory and oblique motions, are accomplished by four pairs of very powerful muscles; these are antagonised by muscles comparatively feeble and indirect in their application.

The closure of the jaws is effected by the masseters and the temporals, attached to the outer sides of the jaw; and the external and internal pterygoids, attached to its inner sides.

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(1) Pterygoid muscles. 1. Upper, and 2. Lower heads of external pterygoid muscle. 3. Internal pterygoid muscle.

The masseter, temporal, and internal pterygoid muscles close the jaws and press the teeth against one another, and this is their principal action. They are antagonised by the digastric, the mylo-hyoid, and the genio-hyoid muscles, which, aided perhaps by the platysma, depress the lower jaw when the hyoid bone is fixed by its own depressor muscles.

The external pterygoid draws the jaw forward, and so in some measure tends to open it; as the two muscles do not always, or indeed generally, act together, they give a lateral movement to the jaw. The superficial portions of the masseter and the internal pterygoid are ordinarily supposed, as their direction is slightly backwards, to assist in drawing the jaw forwards; but Langer, a recent investigator of their action, attaches very little importance to this, and indeed considers that, when the jaw has been pulled forwards by the external pterygoid, the combined action of the internal pterygoid, the temporal, and the masseter, may bring it back again.

In ordinary mastication the various movements are combined in every possible manner.

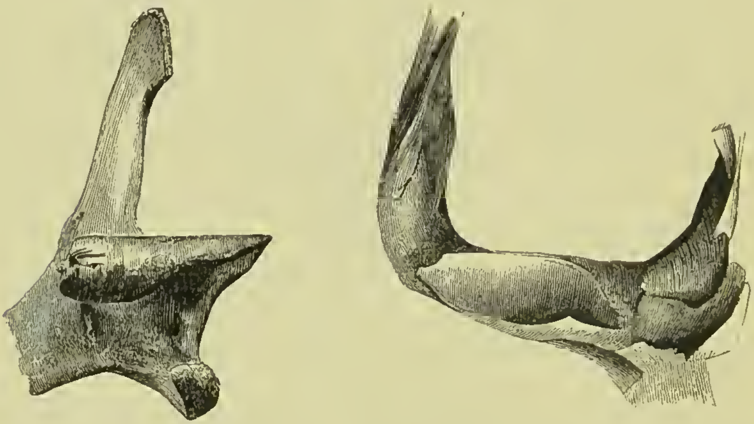
When the mouth is widely open the condyles play upon the articular eminence in front of the glenoid cavity, and the external pterygoid, which assists in widely opening the mouth, draws not only the condyle, but also the interarticular fibro-cartilage forwards, so that the latter still intervenes between the condyle and the articular eminence. The interarticular cartilages do not, however, accompany the jaw in its extreme movement, but are believed only to pass forwards as far as that part of the eminence which is slightly hollowed out. As, however, in dislocation they accompany the condyles, this supposition may be incorrect.

The position of repose is neither complete closure nor opening of the jaws: in persons with enlarged tonsils the habitual position is one with the mouth somewhat more widely open, owing to the difficulty of breathing through the nose; a fact which perhaps is one cause of an irregularity in the disposition of the teeth.

The axis on which the jaw moves is, owing to the bend of the ramus, far behind the glenoid cavity; it lies very nearly in a plane formed by prolonging the plane of the masticating surface of the teeth.

The motions executed in mastication differ much according to the nature of the food; hence it happens that in different animals the muscles of mastication are very variously developed.

Figs. 263, 264 (1).



Thus, in the Herbivora, which move their jaws greatly from side to side, as anyone may observe for himself, the pterygoids, and especially the external pterygoid, attain to a very large relative size.

On the other hand, in the Rodents, which move their jaws backward and forward in gnawing, the masseter is enormously developed, and has a very marked general backward direction.

Although it is not strictly true, the masseter and temporal may be said in mammals to be developed in an inverse ratio to one another: when one is large the other is not.

The masseter is at a maximum in Carnivora, which have

(1) Condyle of the lower jaw, and glenoid fossa of a tiger.

little lateral movement possible to their jaws; the temporal is also highly developed in many of the class.

In the great apes, the temporal becomes enormously developed only at the period of second dentition; this fact, conjoined with its size, which in Herbivora seems to have some relation to the presence or absence of canines, would incline one to suppose that it was useful in that rapid closure of the mouth appropriate to biting when animals fight or seize prey.

The form of the glenoid cavity also bears an intimate relation to the dentition of the animal, and the nature and extent of the movement of its jaws.

Thus, in a child it is nearly flat, with no well-marked surrounding elevations; its axis is transverse, and little rotary motion is made use of. In the adult it is deeply sunk: the axis of the condyle is oblique, and rotary movements are largely made use of in triturating food.

In the Felidæ, it is strictly transverse; their teeth, adapted for slicing but not grinding, would gain nothing by lateral motion, which is rendered quite impossible by the manner in which the long transverse condyles are locked into the glenoid cavity by strong processes in front and behind. Curiously enough the interarticular cartilage is present, but as the condyle never moves forward, the cartilage is not attached to the external pterygoid muscle.

In Herbivora the condyle is roundish, the ascending ramus long, the pterygoid muscles large, and the glenoid cavity shallow; in the whale, which of course does not masticate at all, there is no interarticular cartilage, and no synovial membrane; the articulation is reduced to a mere ligamentous attachment.

In Rodents there is no post-glenoid process, so that the condyles have a large play backwards, useful for employing the teeth in gnawing.

The harder a substance is, the farther back between the molars it is placed; and as the food escapes from between the teeth it is constantly being replaced by the lips, cheeks, and tongue, the buccinator muscle being largely concerned in this work of preventing morsels of food from escaping from the teeth during its mastication.

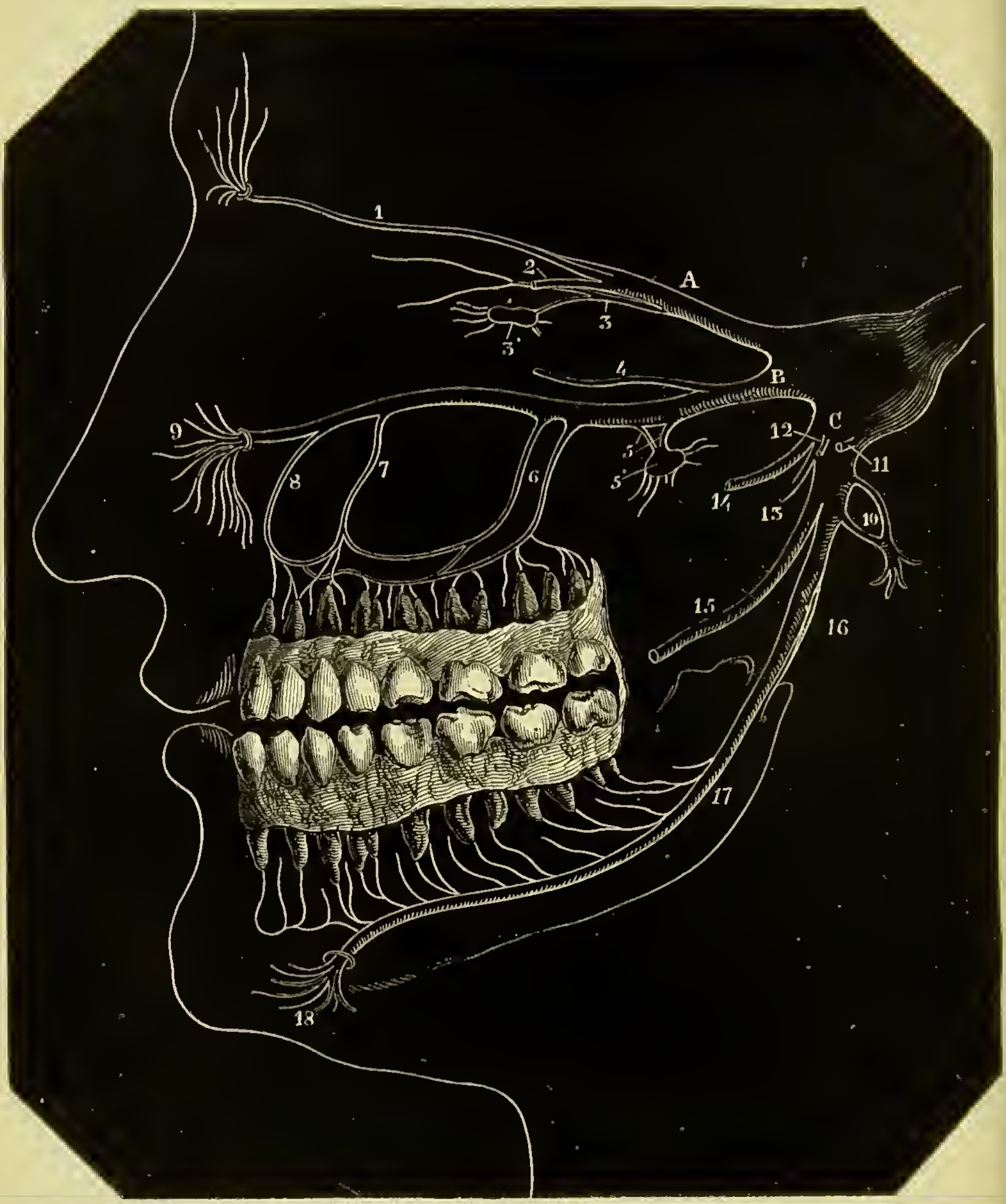
Just as the muscles of mastication vary in their relative development in accordance with the food to be dealt with, so also do the salivary glands.

As a rule herbivorous creatures have large parotid glands; that is to say, those creatures which deal with the driest food and masticate it the most have this gland largely developed. For instance, it is very large in Ruminants; in herbivorous Marsupials it is larger, in the carnivorous section smaller, than the submaxillaries. When an especially viscid fluid is required, as, for example, that which lubricates the tongue of an ant-eater, this is furnished by exceedingly large submaxillary glands.

The face is to a very great extent modelled by the form of the maxillary bones, and these again are found to be largely influenced by the dentition of the animal, so that it comes to be true to say that the face of an animal largely depends upon its dentition. Thus, to take a lion as an example, the snout is broad owing to the wide separation between the canines, which gives them a good purchase in grasping a living prey; its shortness enables them to be used at a greater mechanical advantage than would be the case were they further removed from their fulcrum at the joint, and the breadth of the face below the eyes is conferred by the widely spreading zygomatic arches, which are obliged to be wide to give passage to the very powerful temporal muscles, and attachment to the masseters.

Without going into further details, which the reader can readily supply for himself, it will be seen that the contour of the face is largely determined by the dentition in this instance, and it is in marked contrast with the long thin snouts of the insectivora, whose forceps-like front teeth as a rule merely pick up unresisting prey, or with the long weak snouts of the horse and the Herbivora generally. The face of the boar, again, is largely determined by the great muscles which move the jaw, and by the bony processes which give attachment to them.

Fig. 265 (1).



(1) Diagram of the Distribution of the Branches of the Fifth Nerve.
(From Tomes' "Lectures on Dental Physiology and Surgery"—drawn by the late Mr. C. De Morgan.)
A. Ophthalmic division :—1. Frontal. 2. Nasal and long ciliary. 3. Branches to ciliary ganglion.
B. Superior maxillary division :—4. Orbital { temporal / malar } 5′. Spheno-palatine (Meckel's) ganglion.
6. Posterior dental, passing down. 7, 8. Anterior dental. 9. Infra-orbital.
C. Inferior maxillary division :—10. Auriculo-temporal. 11. Masseteric. 12. Deep temporal. 13. Pterygoid. 14. Buccal to buccinator, &c. 15. Gustatory. 16. Mylo-hyoid branch. 17. Inferior dental. 18. Mental.

[*To face p.* 559.

If you extend the jaws forward a little, project the teeth, and widen the mouth in man, you get a coarse animal type of face; and, conversely, by a reduction of the maxillary region, perhaps even below the limits which will afford space for the regular disposition of the teeth, you get a refined oval type of face. The jaws of a negro are large relatively to the cranium, as are also those of exceptionally big men, such as we call giants, though this is not universally true; in rickets the reverse is the case.

The nerves of the teeth are derived from the branches of the fifth nerve, the nerve of sensation of the whole side of the face and head: the lower teeth through the inferior maxillary nerve, the upper through the anterior and posterior dental branches of the superior maxillary nerve. The nerves are given off from the nerve trunks in bundles corresponding in number to the roots of the teeth for which they are destined. For the details of the distribution of the fifth nerve the student must refer to works treating of anatomy, as it would be out of place to enter upon the subject at length in these pages, in which merely one or two matters of special interest to the dental student will be touched upon.

Modern researches into the development and the morphology of the nervous system have led to some inferences which, if established, are of much interest to the dental student. The fifth nerve has often been compared to a spinal nerve, with its anterior motor portion, and its posterior sensory portion with a ganglion upon it. But according to Dr. Gaskell ("Proc. Roy. Soc.," Vol. XLIII., 1888, and "Journal of Physiology," Vol. X.), this is not at all a correct comparison; he believes that the third, fourth, and portio minor of the fifth, the sixth and seventh cranial nerves were all once complete segmental nerves with motor and sensory roots, but that their sensory roots with their ganglia have degenerated, though traces of the nerve cells of the ganglia may still be found at their points of emergence.

Hence the portio major, or sensory portion of the fifth, is not the sensory root of the fifth nerve—the motor portion once had its own and has lost it. But, on the other hand, it has taken over the work of the lost sensory portions of the whole set enumerated above, of the motor parts of the fifth amongst them. Hence its very wide connections along the base of the brain and medulla, its origins reaching along the posterior cornua as far down as the cervical region, where it has somewhat similar relations with the hypoglossal, glosso-pharyngeal, vagus, and spinal accessory. Although these have afferent or sensory fibres of their own, as regards the viscera, Dr. Gaskell believes that as regards muscles and organs of animal life their afferent nerves are to be sought in the fifth. The subject is too complex for discussion in these pages, but if these views be correct some of the puzzling phenomena of reflex pain, &c., which are manifested by the fifth nerve become more explicable.

In the case of the inferior maxillary nerve the roots of the teeth come into very close proximity with the main trunk of the nerve; this is especially the case with the lower wisdom teeth. Within a few days of writing these lines I extracted a lower wisdom tooth (with forceps) for a gentleman, who, immediately after the extraction, inquired if he could have bitten his lip, as it felt swollen; on testing it I found slight but well-marked numbness on that side of the lip and chin, which did not wholly subside before he left me. In this case a groove upon the under surface of the much curved roots appeared to indicate that the nerve trunk was in close contact with the tooth.

No reason is at present known why the tooth pulp should be so richly supplied with nerves, unless it confers greater tactile sensibility upon the whole tooth. Teeth with persistent pulps which go on growing throughout the life of the animal, have always large nerves: thus a very large trunk goes to the pulp of a rodent incisor. But although in this case the rich nervous supply doubtless has to do with nutrition, and presides over the great formative activity of the tissue, this does not fully account for the pulps of the teeth of limited growth being so amply supplied with nerves.

As has been mentioned in the description of the lower maxillary bone, the inferior dental nerve emerges from the bone by the mental foramen, near to the end of the roots of the bicuspid teeth. Pain due to distant causes is often referred to the point of emergence of a nerve, as is so frequently exemplified in supra-orbital neuralgia; in the same way pain due to diseased teeth far back in the lower jaw (especially to wisdom teeth), is frequently referred to the bicuspid region. Curiously enough, though there is no apparent close parallel in the disposition of the nerves, a similar reference of pain to the bicuspid region is occasionally observed in the upper jaw. And it may be added that there is very probably some closer parallel in the minute disposition of the nerve centres for the teeth in the upper and lower jaws than is recognisable by rough anatomical processes, for while, to all appearance the nerve trunks are differently arranged, it is a matter of almost everyday observation to find pain due to one tooth referred with precision to its fellow in the other jaw.

The lower teeth derive their vascular supply from the branches given off to each tooth by the inferior dental artery, itself a branch of the internal maxillary; the upper teeth derive their arteries from the superior dental, a part of the alveolar branch of the internal maxillary, which supplies the molar and bicuspid teeth; and the front teeth from the descending branch of the infra-orbital, the vessels thus having an arrangement somewhat analogous to that of the nerves.

The distribution of the veins corresponds closely to that of the arteries.

No lymphatics have been traced into the teeth, though lymph spaces are described by Dr. Black as existing in the alveolar dental periosteum. This, however, is doubtful, as another explanation has been given of the appearances observed. (Cf. p. 107.)

CHAPTER XVI

THE TEETH OF MARSUPIALIA.

The great sub-class of Marsupials, consisting of animals very sharply marked off from placental Mammals by many striking peculiarities, and amongst others by the very helpless condition in which the fœtus is born, was once very widely distributed over the globe. Now, however, Marsupials are numerous only in Australia, where they are almost the sole representatives of the Mammalian class ; there are a few Marsupials elsewhere, as in America (Opossums) and New Guinea ; but there are no Marsupials in Europe, most parts of Asia, and Africa.

It was once supposed that a good many Mesozoic mammals known only by their jaws were Marsupials, but some doubt is now felt upon the subject, as they may have been Monotremes. The opinion held that although Marsupials in former ages were very widely distributed, placental mammals are not descended directly from them, is gaining ground.

The Marsupials of America are all Opossums (*Didelphidæ*), and this family is not represented in Australia. There is evidence to indicate that the Marsupials of America have nothing at all to do with the Australian Marsupials, but were derived from a different source, at the time when Marsupials abounded all over Europe.

The Marsupials of Australia almost monopolise that country ; thus Mr. Wallace says of it : “ The Australian region is broadly distinguished from all the rest of the globe by the entire absence of all the orders of non-aquatic mammalia that abound in the old world, except two—the Winged Bats (*Chiroptera*) and the equally cosmopolite Rodents. Of these latter, however, only one family is represented—the Muridæ—(comprising the Rats and Mice), and the Australian representatives of these are all of small or moderate size—a suggestive fact in appreciating the true character of the Australian fauna.

“ In place of the Quadrumana, Carnivora, and Ungulates, which abound in endless variety in all the other zoological regions under equally favourable conditions, Australia possesses two new orders or sub-classes, Marsupialia and Monotremata, found nowhere else in the globe, except a single family of the former in America.

“ The Marsupials are wonderfully developed in Australia, where they exist in the most diversified forms, adapted to different modes of life. Some are carnivorous, some herbivorous, some arboreal, others terrestrial. There are insect-eaters, root-gnawers, fruit-eaters, honey-eaters, leaf or grass-feeders.

"Some resemble wolves, others marmots, weasels, squirrels, flying squirrels, dormice or jerboas.

"They are classed in six distinct families, comprising about thirty genera, and subserve most of the purposes in the economy of nature fulfilled in other parts of the world by very different groups; yet they all possess the common peculiarities of structure and habits which show that they are members of one stock, and have no real affinity with the old-world forms, which they often outwardly resemble."—"Geographical Distribution of Animals," p. 391.

I have quoted this passage from Mr. Wallace, because much of it is applicable to the teeth.

In Australia, the present home of the marsupials, representative species abound; that is to say, widely different though the animals really are, there are many genera and species which have the habits of, and, as it were, fill the place of such creatures as the Carnivora and Insectivora and Rodents amongst the placental mammalia. And not only do they possess something of their habits and external configuration, but in those characteristic structures which are subservient to the creature's immediate wants, the marsupial representatives closely mimic the more highly organised placental mammals. Thus the teeth of an insect-eating marsupial very closely resemble those of a true Insectivore, though retaining certain eminently marsupial characters; in the same way the dentition of the marsupial Thylacine mimics that of a dog. (Compare Figs. 267 and 268.)

And although marsupial dentitions do vary very much, yet there are many transitional forms by which we are sometimes able to trace the successive modifications through which extreme divergence has been ultimately attained.

Just as we ascribe to placental mammals the formula—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{4}{4}\;m\,\frac{3}{3}=44$$

as the typical or parent dental formula, so recent marsupials possess the following—

$$i\,\frac{3}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{4}{4}=44.$$

An excess over these numbers is, however, more common than in placental mammals; thus, the opossums have ten incisors in the upper and eight in the lower jaw; the Thylacine, very dog-like in its dentition, has eight upper incisors, whilst the little ant-eating Myrmecobius mounts to a total of fifty-two or fifty-six teeth, having eight or nine molar and premolar teeth on each side of the jaw.

Though no living marsupial has more than three premolars, it has been presumed that four was the original number, as in placental mammals, and Mr. Oldfield Thomas has found in Dasyurus and in Phascologale dorsalis a fourth tooth, in the position of pm_2; he infers, therefore, that it is pm_2 which has been lost by recent marsupials, and further points out that a marked gap exists in this situation in Didelphys, Perameles, and others.

Mr. M. Woodward ("Proc. Zool. Soc.," 1893) has examined by means of serial sections, as well as by clarifying the whole jaws in clove oil, a very fine series of marsupial embryos. He has found that in Petrogale (one of the kangaroo family) there are no less than six incisors in the premaxillary bone, of which three were minute calcified vestigial teeth, while the other three were in the stage of tooth germ only, but were of far larger size.

But though after careful investigation he was fully convinced that they were not teeth of two dentitions, but that they, like the rest of the functional series, certainly all belonged to the first or milk series, he has now partly abandoned this view.

Moreover, he holds that there are five premolars; this is less of a difficulty than it would otherwise be, as the recent Myrmecobius has eight or nine cheek teeth on each side, and the ancient Amphilastes had twelve, of which, judging by form, six would be classified as premolars. To this question we shall have to recur in discussing the question of their milk dentition.

Though the total number of functional back teeth is the same as in placental mammals, the marsupial has only three premolars and has four true molars. The premolars (false molars) differ from the true molars in the greater simplicity of their crowns, just as in most placental mammals; but, although, looking at the complete adult dentitions, no hesitation would be felt in classing the teeth under the heads of premolars and true molars, yet there is a curious anomaly in the succession of the teeth which applies to the whole of the sub-class Marsupialia, and to some extent invalidates the definition of "premolar" as applied to their teeth. Only one of the premolars (the hindmost) has vertically displaced another tooth. From this it was at first argued that the whole milk dentition of marsupials consists of four milk molars (one on each side of each jaw), there being no succession among incisors nor canines in any known marsupial. It was further pointed out by Sir W. Flower, who was the first to fully describe these peculiarities in the succession of marsupial teeth ("Phil. Trans.," 1867), that the extent to which the solitary displaced molar is developed varies much in the different families: no trace of any succession had been observed in the Wombat (cf. p. 568); in the Thylacine (a dog-like creature) the small deciduous molar is calcified, but is absorbed or shed prior to any other teeth being erupted; whilst in the Kangaroos it is retained till a much later period (see p. 579), and in the Kangaroo Rat (Hypsiprymnus) the deciduous molar has not yet given place to its successor at the time when the last permanent molar has come into place, so that it for a long time ranges with the other teeth and does work.

This subject has been further investigated by Mr. Oldfield Thomas, who has found that the Dasyuridæ present the same deciduous dentition as the other families, that is to say, that some have a well-developed deciduous molar, and that it occurs in various phases of reduction, some having none at all. ("Phil. Trans.," 1887.) This author, writing of Phascologale, one of the Dasyuridæ, says—

"The normal state of a member of this group is to have three well-developed premolars, the last one of which has a (milk) predecessor. Then a tooth reduction has taken place, all of which has fallen upon what is evidently a peculiarly plastic tooth, *i.e.*, pm_4, and this, with the (milk) tooth preceding it, has been decreased in various degrees and in the end suppressed, as in the allied genera Dasyurus and Sarcophilus." (Oldfield Thomas.)

Those species which have a large pm_4 have preceding it a tricuspid (milk) tooth, but as pm_4 gets reduced, the tooth preceding it is reduced still faster till it quite aborts; even then the pm_4 presents the peculiarity of not being erupted, and indeed not being calcified, until later than the other teeth.

This peculiarity of the possession of a single changing tooth was fully established even in Mesozoic times, as is exemplified in Triconodon and other Mesozoic marsupials.

The question whether the tooth change of the marsupials is the remnant of a more complete change in an ancestral form, or is the dawning of a more complete change, as believed by Flower, was discussed at length by Mr. Oldfield Thomas.

That it is the first formation of a change he formerly held strongly, (i.) because the marsupials are at a lower stage of evolution than other mammals, and so it would be unlikely that they had once evolved a change, and then evolved it away again; (ii.) because five out of the six marsupial families have precisely the same amount of tooth change, which would be unlikely if it were an atavism; (iii.) and, because no fossil marsupials present any indication of a fuller change, but have just the same.

But in the face of the discoveries of Kükenthal, Röse, Leche and others, Mr. Oldfield Thomas has abandoned this position, and accepts the view as now incontestable that the functional dentition of marsupials is homologous with the milk dentition of true Diphyodonts, there being a single permanent or successional tooth developed on each side of the jaw

But before entering further upon this question, it is desirable to clear up if possible the homologies of the whole functional set of teeth of marsupials. With regard to this, the most diverse opinions have, and still do, prevail.

When it was discovered by Sir W. Flower that there was a vertical succession of one tooth only, the last of the premolar series, it was at first thought that all the rest of the functional teeth, with the one exception, corresponded to the permanent teeth of other mammals; and that there was a milk dentition consisting of one tooth only, variable in the extent to which it was developed, so that it was regarded as presenting the first appearance of a milk dentition. There were many difficulties in the way of accepting this view, which was nevertheless adopted by Mr. Oldfield Thomas in his elaborate paper on the Dasyuridæ. But Kükenthal and Röse, investigating serial sections of the jaws of young animals, found that the dental lamina presented swellings to the lingual side of the developing functional tooth germs, which they interpreted as being aborted permanent teeth, and hence they came to the conclusion that the whole of the functional set must be regarded as the milk teeth, and that the permanent teeth were suppressed. And this view was cordially accepted by Mr. Thomas, who abandoned his earlier ideas on the subject.

The molars, originating from the dental lamina and never having had any predecessors, they regard also as belonging to the milk series, just as they regard them in other mammals.

This general idea, that the functional teeth really represent the milk dentitions of other mammals (with, perhaps, the solitary exception of the one replacing premolar) has gained somewhat general acceptance; and the various other phenomena presently to be described it has been sought to explain in accordance with this hypothesis.

Woodward ("Proc. Zool. Soc.," 1893) discovered that in some of the Macropidæ there were a number of small calcified teeth, in addition to the tooth germs of the functional teeth.

In Petrogale he found, in addition to the tooth germs of the three functional incisors, three minute but calcified rudiments in the upper jaw, and two in the lower; whilst accepting the view that the functional incisors were of the milk dentition, he regarded the rudiments which he discovered as belonging to this series, that is to say, he considered that they represented additional suppressed teeth; and hence as indications that the polyprotodont marsupials had six incisors on each side in the upper jaw. Subsequently, however, he adopted Leche's interpretation that they were premilk teeth.

Leche ("Morpholog. Jahrbuch," 1893, and "Entwickelungs Geschichte des Zahnsystems, Bibliotheca Zoolog.," 1895) described in Myrmecobius the occurrence of calcified rudiments which lay to the labial side of the functional tooth germs, and therefore were referable to an antecedent set of teeth. Bound by the idea that the functional teeth are milk teeth, he is compelled to assume that these rudiments are referable to a premilk series, and this interpretation is accepted by Woodward, who discovered some additional calcified rudiments, and holds that he has found confirmation of this by the discovery of similarly placed rudiments in Phascologale.

It will be seen that so far the interpretation of the homologies of the functional teeth turns wholly upon the degree of significance which is attached to the observations of swellings of the tooth band to the lingual side of the functional tooth germs; that is to say, to the observations of Röse and Kükenthal, who interpreted them as unquestionable tooth germs, and whose interpretation has so far been accepted almost without question.

But if these are not real tooth germs, that is to say, if they are only swellings such as may occur in the residual tooth band without such definite significance, the whole case falls to the ground.

And this question is strongly raised by Messrs. Wilson and Hill, of Sydney, who, in an exhaustive paper upon the development of the teeth in Perameles, have ably summarised the whole matter (and of whose summary I have made much use).

They hold that, using the criteria laid down by Leche (who, however, has not been led to this conclusion by his own criteria), there is no adequate evidence that the differentiation of these swellings is sufficient to entitle them to be considered as tooth germs, and hence that there is no evidence that Leche's Myrmecobius tooth rudiments are to be regarded as premilk, but that it is a far simpler and less far-fetched interpretation that they, as well as the germs observed by themselves, by Woodward and others, are ordinary milk teeth.

Hence their conclusion is that the functional dentition of marsupials is the permanent dentition of other mammals, and that the milk dentition is the one upon which suppression has fallen in varying degrees of completeness; and this conclusion had already been arrived at by Dr. Marett Tims ("Anat. Anzeig.," 1896, and "Trans. Linnean Soc.," 1896). The marsupials, according to them, are to be regarded as truly diphyodont mammals, in whom the milk dentition, not wanted owing to the peculiar conditions of the birth of the young and their long sojourn in the pouch attached to the teats of the mother, has practically vanished.

This view, if adopted, greatly simplifies the whole question, and is the one to which I am myself inclined from a study of the various papers published upon the matter; it, of course, does away with the somewhat improbable assumption of a "premilk" dentition.

The observations of Röse upon the early conditions of the Wombat are important in this connection; he found that there were rudiments of calcified teeth entirely unrepresented in the functional dentition, and that these belong to a generation of teeth antecedent to the functional teeth. Moreover, he finds in the place subsequently occupied by the single persistent premolar, a precociously calcified tooth with a large germ to its lingual side, which he regards as the germ of the functional tooth.

To fit in these observations with the widely accepted views as to the functional teeth of marsupials being the milk teeth, leads into difficulties, and Röse himself frames the far-fetched hypothesis that in the Wombat there is a difference in the homologies of the teeth in the front and the back of the jaw, and so that the Wombat stands very much alone in a very exceptional condition as regards its dentition. Leche, on the other hand, sets aside Röse's difficulties (arising from his feeling compelled to regard the calcified precocious germs of the front of the jaw as true milk teeth), and relegates the functional teeth of the Wombat to the milk dentition.

So far, for the sake of clearness, nothing has been said about the homologies of the last premolar of marsupials and of its deciduous predecessor.

Here again the views of Wilson and Hill commend themselves as the simplest : they regard the deciduous tooth as a true milk tooth, ranging with the other calcified and uncalcified milk rudiments (premilk of Leche and Woodward), and point to the fact that it, like them, is in some cases clean gone, as in Dasyurus, though even in Dasyurus it is present as a calcified vestige in the mammary fœtus, while in Thylacinus the successional premolar is a well-developed tooth, and is preceded by a minute and rudimentary milk tooth shed in infancy.

Hence they hold that there is a process of reduction affecting first the milk tooth, and finally both the milk tooth and its successor as in Dasyurus, and that this process of reduction is the same that has affected all the other milk teeth ; it is the hindmost member of the milk series, and upon it reduction has come last and so less than upon the more anterior milk teeth.

For the curious fact that there is a succession at one point in the jaw only, Mr. Oldfield Thomas suggested as an explanation, that there first took place a retardation of a back permanent tooth, perhaps useful for "packing" purposes in a jaw as yet small, and that when the retardation had gone to a certain point, a milk tooth was developed to fill the gap in the series which would otherwise have existed.

A different light was thrown upon the subject by the very interesting paper of Mr. Woodward : he finds that even the successional tooth germ also develops from the primitive tooth band, between pm_3 and pm_4 as they are usually supposed to be : he therefore believes that it really belongs to precisely the same series as the others, and that it is delayed by being crowded out. This suggestion, *i.e.*, that it really belongs to the same series as the other teeth, this being the milk series, seems much more probable than that just one single tooth of a different series should attain to the very full development that it does in some genera.

Röse comes somewhat near the same idea, as he urges that in some species of Didelphys, Perameles, &c., it has been shown that no tooth change takes place after the rule laid down by Flower and Thomas, but that a late tooth thrusts itself up into the row between two of the others without the absorption of any of them, so that the question arises whether there is any real tooth change in marsupials, in the ordinary accepted sense of the word.

Leche has apparently adopted the belief that the single tooth change is the herald of a new dentition, but he holds to the idea that the functional teeth are milk teeth, and regards the epithelial swellings of Kükenthal and Röse not as remnants of a lost second set, but as heralds of a second set not yet acquired by the marsupials.

The question is, however, far too lengthy for discussion in these pages. For further information upon it the reader is referred to Messrs. Wilson and Hill's able summary, to Leche, and to the papers of Messrs. Kükenthal, Röse, and Woodward.

A further peculiarity of the marsupials is the structure of their enamel, which is penetrated by the dentinal tubes. My father, some years ago, described and figured the teeth of a large number of marsupial genera ("Phil. Trans.," 1850), and found that although in the different families the tube system of the enamel varied in its richness and in the depth to which the tubes penetrated, yet it was conspicuously present in the whole class, with the sole exception of the Wombats, in whom nothing of the kind is to be found. The dilatation noticeable at the boundary line of the enamel and the dentine (see Fig. 266) is a kind of clumsy joint brought about by the coalescence at this point of the tube-forming cells—on the one side odontoblasts, on the other enamel cells.

The extent to which the tube system exists in the enamel varies much in different families: it attains its utmost development in some macropores, and is more feebly present in some Dasyuridæ, whilst in Myrmecobius, and yet more in Tarsipes, it is reduced to small limits.

The dilatation is not universally present, but a well marked curve at the juncture of the enamel and the dentine sometimes occurs, as well as various curves in the course of the tubes through the enamel.

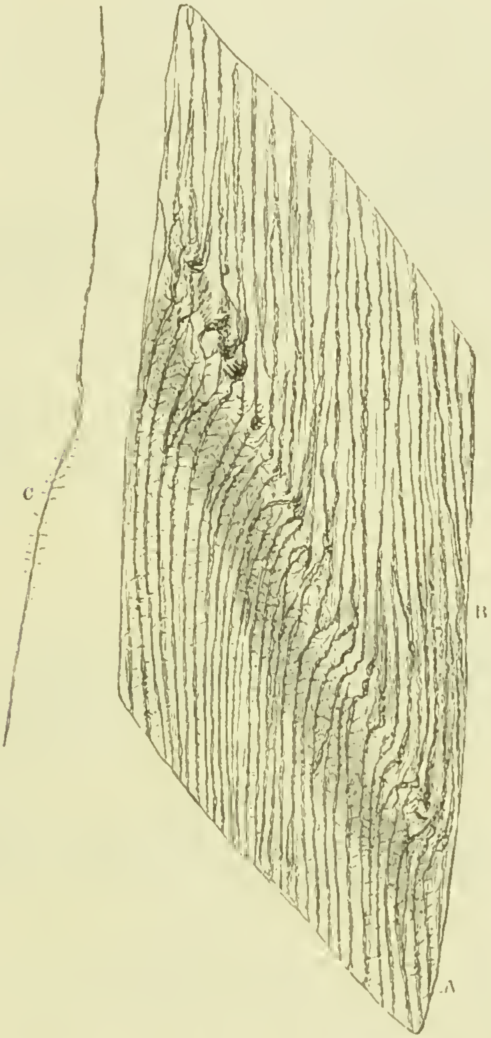
It is said by von Ebner that the tubes in marsupial enamel are not in the axes of the prisms, but run between them, but this is a point upon which it is a little difficult to be certain; and I am of opinion that the tubes are in the substance of the prisms. (See p. 30.)

The Marsupials are grouped into:—

Polyprotodonts. Incisors numerous, small and subequal; canines pronounced; and molars strongly tuberculated, in many sharp cusped, *e.g.*, Didelphys.

Diprotodonts.—Incisors not more than $\frac{3}{3}$, often $\frac{3}{1}$ and

Fig. 266 (1).



(1) Enamel and dentine of a kangaroo (Macropus major).
The dentinal tubes in the dentine (A) are furnished with numerous short branches at the line of juncture with the enamel ; they are dilated, and a little bent out of their course, while beyond the dilatation they pass on through about two-thirds of the thickness of the enamel in a straight course and without branches. Only a part of the whole thickness of the enamel is shown in the figure. B. Enamel penetrated by the tubes. C. Individual dentinal tube.

sometimes as low as $\frac{1}{1}$. The first upper and the lower incisors are large, with cutting edges.

Upper canines absent or small, lower absent. Molars bluntly tuberculated or ridged, *e.g.*, Kangaroo. Under the Diprotodont division come the Wombats, which have all their teeth with persistent pulps, and their incisors, rodent-like, with enamel on their front surfaces only.

Among the Polyprotodont series there exists one genus of flesh-eating marsupials whose ferocity is such as to have gained for them the names of wolf and tiger, while the resemblance of the head to that of a dog has given origin to the popular name of "dog-headed opossums" (1).

The resemblance to the dog in dentition is even more close than in external form; whilst retaining certain marsupial attributes, the teeth of the Thylacine are, so far as their working capabilities go, almost exactly like those of the dog. The dental formula is—

$$i\,\frac{4}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{4}{4}.$$

The incisors are small, close set, and sharp edged, the outermost being somewhat caniniform. The canines are stout, pointed teeth, not quite so long relatively as those of a dog. The premolars are conical teeth, implanted by two roots, and very similar to those of the dog; they are followed in the upper jaw by four molars, increasing in size from the first to the third, but the last true molar is again a smaller tooth.

The upper molars are all of the "carnassial" pattern; there is a "blade" elevated into subsidiary cusps, and internally to this a "tubercle," supported by a thin root.

The lower molars also bear some resemblance to the carnassial teeth of the dog, consisting of a strong, sharp-edged blade, with anterior and posterior subsidiary cusps, the latter being somewhat broad and tubercular.

---

(1) It has, of course, no real relationship to the true opossums, which are not found in Australia.

An allied animal (Dasyurus ursinus), though smaller than the Thylacine, and having teeth of a less sectorial character, is so destructive to sheep and so fierce and untamable, that it has earned the name of "Tasmanian Devil."

Within the limits of the same genus, a species (Dasyurus viverrinus) is to be found, in which the molar teeth are studded over with long sharp cusps, like the teeth of Insectivora, a group which it resembles both in its habits and food.

FIG. 267 (1).

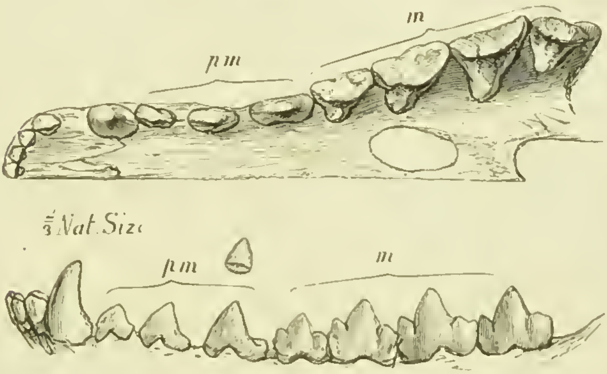
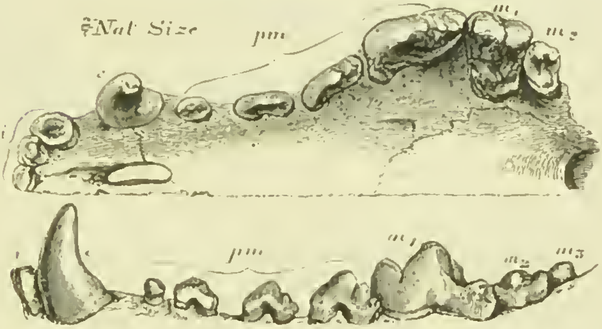


FIG. 268 (2).



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(1) Upper and lower teeth of the Thylacine. The rudimentary milk molar, which is absorbed before birth, has been placed over the third or last of the premolars, which succeeds to it vertically.

(2) Upper and lower teeth of a dog, which are placed side by side with those of the Thylacine, to show the many points of resemblance between the two dentitions.

A number of smaller marsupials approximate in their dentition more or less to the Insectivorous type, whilst a tolerably complete chain of existing forms serves to bridge over the gap between the rapacious Dasyuridæ and the herbivorous Kangaroos and Wombats.

Amongst the Opossums the larger species have large canines, and the dentition in its general features approximates to the Dasyuridæ; they feed upon birds and small mammals, as well as upon reptiles and insects, though the smaller species are more purely insectivorous.

Myrmecobius, a small Australian marsupial of insectivorous habits and dentition, is remarkable as having teeth in excess of the number of the typical mammalian dentition, having—

$$i\,\frac{4}{3}\;c\,\frac{1}{1}\;p\,\frac{3}{3}\;m\,\frac{6}{6},$$

though of course there is a doubt as to their division into premolars and molars.

It is further remarkable in that its milk (or premilk?) rudiments are carried further than those of most other marsupials. Leche described calcified predecessors to $i\,\frac{1}{\ }$, $i\,\frac{2}{\ }$ and to $i\,\frac{\ }{2}\,\frac{\ }{c}$ and an uncalcified predecessor to $i\,\frac{\ }{3}$, and to these Woodward added $\frac{i}{\ }\,\frac{3}{\ }$, $\frac{i}{\ }\,\frac{4}{\ }$ and $\frac{c}{\ }$: in the lower jaw he found the same as Leche, and also well differentiated germs of $\frac{\text{dpm } 4}{\text{dpm } 4}$, so that its full milk (or premilk?) formula was—

$$i\,\frac{1234}{23}\;c\,\frac{1}{1}\;\frac{\text{dpm } 4}{\text{dpm } 4}.$$

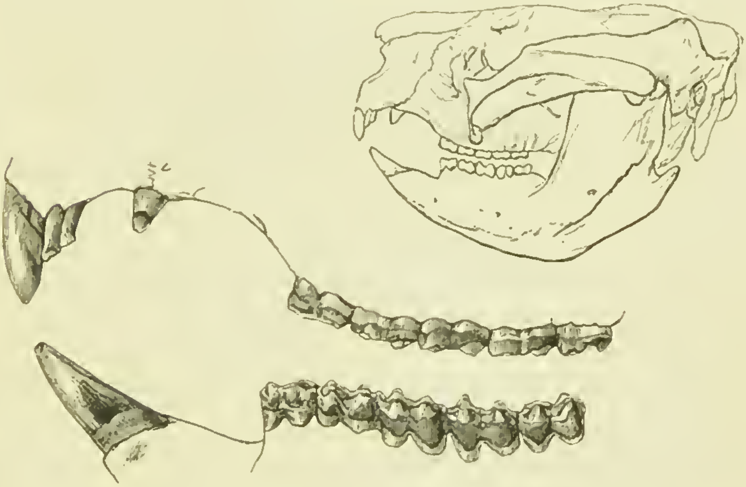
The deciduous premolar would not of course be included by Leche and Woodward with their "premilk" teeth, but according to Wilson and Hill it should be included in a milk dentition.

In the Phalangers, nocturnal arboreal animals found in

Australia and a part of the Malay Archipelago, the canines though present, are feeble ; an interspace also separates the incisors from the molar series.

The lower incisors, reduced to a single pair, are procumbent, and grow from persistent pulps; there is thus functionally some faint approach to the character of a rodent dentition, as may be seen by an inspection of the foregoing figure, though there is a strongly-marked transverse condyle to the lower jaw. Phascolarctos cinereus has been shown by Mr. Oldfield Thomas to have the same reduced deciduous tooth as Thylacinus.

FIG. 269 (¹).



The very sharp cusps of the molars, in the lower jaw somewhat concave on their inner aspect, are so formed as to long preserve their sharpness and accurate co-adaptation.

The name "Kangaroo Rats" (Hypsiprymnus) is applied to a genus consisting of about a dozen species ; they are all small creatures, not much larger than rabbits, but having the general proportions of Kangaroos. They are quiet, gentle little creatures, of strictly herbivorous habits, and

---

(¹) Teeth of Phascolarctos cinereus. An outline figure of the skull is placed above to show the general "rodent" aspect of the skull.

they are interesting to the odontologist as possessing a dentition which throws some light upon several anomalous extinct forms, whose habits and affinities have been the subject of much controversy.

The dental formula is—

$$i\,\frac{3}{1}\;c\,\frac{1}{0}\;p\,\frac{1}{1}\;m\,\frac{4}{4}.$$

The first pair of upper incisors are sharply pointed, are directed nearly vertically downwards, and grow from persistent pulps. The second and third do not grow from persistent pulps, and their worn crowns do not attain to the same level as those of the first pair.

All three pairs are antagonised by the single pair of large procumbent low incisors, of which the sharp points meet the first pair of upper incisors, while the obliquely-worn surface behind the cutting edges impinges against the second and third upper incisors.

The arrangement of the incisors, and the sharpness of their cutting edges are calculated to effect the same objects as those attained by the incisors of a rodent; a still closer resemblance would be brought about by the dwindling (which occurs in other genera) and final disappearance of the second and third upper incisors, and a compensating extra development of the first pair.

The canines are not large: yet they are not so small as to be termed rudimentary; in the lower jaw they are absent.

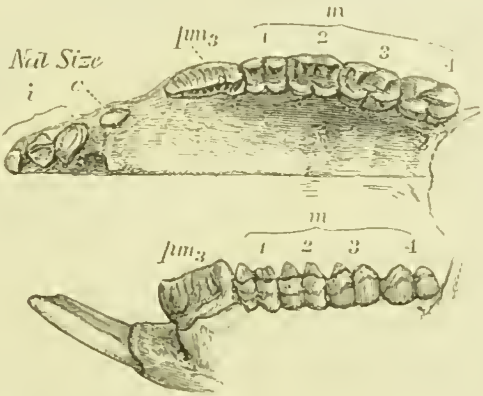
Only one premolar exists in the adult, and this is a very peculiar tooth; its crown is very long from back to front (at least twice as long as any of the molars, and in some species as long as three of the molars), and consists of a finely furrowed blade with a sharp edge; the blades of the upper and lower teeth slide over one another. Behind this there are four true molars, with square quadricuspid crowns, which become much worn down by use.

The last and only premolar, the tooth to which attention has already been drawn on account of its size and other peculiarities, by virtue of its great size displaces not only the usually deciduous molar, to which it is the legitimate successor, but also turns out the premolar in front of it.

In this particular the succession of the teeth in the Hypsiprymnus is the same as that of the true Kangaroo, which may be understood by a reference to Fig. 271.

There are some extinct animals, perhaps marsupials, known only by their jaws, which have been the subject of much controversy. Professor Owen, basing his arguments largely upon the presence of premolars which possessed elongated and sharp-edged blades, held that *Plagiaulax* (cf. p. 328) and *Thylacoleo* were carnivorous, saying of the latter that it possessed the simplest and most effective dental machinery for predatory life known among mammalia; Dr. Falconer, in the case of the first, and Professor Flower in the case of the Thylacoleo, having shown this view to be untenable, or at least unsupported by adequate evidence.

FIG. 270 (1).



A clue to the nature of the great blade-shaped teeth of these extinct creatures is afforded by the form of the premolar of the herbivorous **Hypsiprymnus**. (See Fig. 270.) The incisors were reduced in number, and were large; the teeth between them and the large premolar were stunted;

---

(1) Upper and lower teeth of Hypsiprymnus (Bettongia) (Graii?). The dentition represented is that of the adult animal, the permanent premolar (pm_1 or pm_3 ?) being already in place.

but both these points are true of the herbivorous Kangaroos. The Thylacoleo differs, however, from all known animals by the immense size of the thin-edged premolar (worn flat in aged animals), and by the rudimentary condition of its true molars. But its incisors, lying forwards and closely approximated in the middle line, are particularly unsuitable for catching and holding anything alive and struggling, whilst the nearest resemblance to its blade-shaped tooth is to be found in harmless herbivorous creatures, so that the balance of evidence is much against Professor Owen's view.

The dental formula of Thylacoleo was—

$$i\frac{3}{1}\ c\frac{1}{0}\ p\frac{3}{1}\ m\frac{1}{2}.$$

The first upper incisor was very large, and the second and third very small, as were the canine and the first two upper premolars; but the last upper and the only lower premolars (1) were great blade-shaped teeth like the large premolars of Hypsiprymnus, only far larger.

Thus its useful teeth were only a pair of incisors above and below, and a pair of sectorial premolars.

The **Kangaroos**, comprising many species of very varying size, are (with the exception of a few old males) all docile creatures of herbivorous habits; they in some particulars recall the ruminants.

Their dental formula is—

$$i\frac{3}{1}\ c\frac{0}{0}\ p\frac{1}{1}\ m\frac{4}{4}.$$

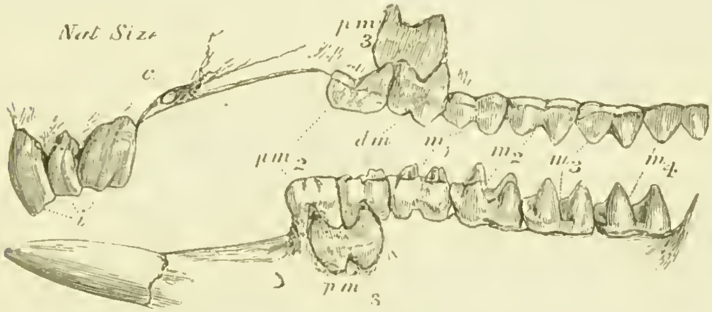
The three pairs of upper incisors are more equal in size than in the Hypsiprymnus, and the central pair do not grow from persistent pulps. The lower incisors are very peculiar teeth: they grow from persistent pulps, are procumbent, projecting forwards almost horizontally, and are very much flattened from side to side, their outer surfaces being but slightly convex, and their inner surfaces flat, with a median ridge. Their margins are almost sharp. There is an unusual amount of mobility between the two halves of the lower jaw, so that these two teeth can be to a slight extent separated from one another.

---

(1) Lydekker suggests that there were other lower premolars present, but they were soon lost.

The upper canine is often present as a very minute rudiment, but in no Kangaroo does it attain to a greater size.

FIG. 271 (1).



The dentition of the Kangaroo is somewhat perplexing to the student, for two reasons: the one, that the premolar not only displaces the solitary deciduous molar, but also, as in Hypsiprymnus, on account of its greater size, the second premolar, which was in front of the deciduous molar; and, besides this, in animals past adult age, teeth are shed off from the front of the molar series till at last only the last two true molars on each side remain.

Thus the dentition of the Kangaroo at successive ages may be thus represented—

$$i\,\frac{3}{1}\;c\,\frac{0}{0}\;p\,\frac{1}{1}\;dm\,\frac{1}{1}\;m\,\frac{4}{4},$$

or, in all, six molar teeth. Then the third premola displaces the second premolar as well as the usually deciduous molar, and we have—

---

(1) Upper and lower teeth of Halmaturus ualabatus. The successional premolar is not yet erupted, and is shown in its crypt; when it comes into its place it will displace the deciduous molar, and one of the anterior premolars as well. In the upper jaw a rudimentary canine is shown. The point of the lower incisor would fit, in closure of the mouth, behind the long anterior upper incisor, but the width of the page did not admit of the teeth being placed in their true relative positions without reduction in size.

$$i\,\frac{3}{1}\;c\,\frac{0}{0}\;p\,\frac{1}{1}\;\text{(a new one)}\;m\,\frac{4}{4},$$

or, in all, only five molar teeth.

Then, one after another, teeth are shed off from the front of the molar series, just as in the Phacochœrus (see p. 396), till all that is left is—

$$i\,\frac{3}{1}\;c\,\frac{0}{0}\;p\,\frac{0}{0}\;m\,\frac{2}{2}.$$

The deciduous molar of the Kangaroo is a fully-developed tooth, which takes its place with the other teeth, and is not distinguished from them by any special characters, so that mere inspection of the jaw of a young Kangaroo having it in place, at the same time with a premolar in front of it and four true molars behind it, would not lead an observer to suspect its true nature.

No existing creature serves to connect the Kangaroos closely with the Wombat, but the extinct Diprotodon appears to have in a measure bridged across the gap.

The Wombats (**Phascolomys**) are heavily-built, inoffensive creatures, which burrow in the ground and subsist largely upon roots. In their dentition they closely simulate the rodents, as they possess but a single pair of chisel-edged incisors in either jaw, growing from persistent pulps, and embedded in very deep and curved sockets. These differ from the corresponding "dentes scalprarii" of true rodents in that there is a complete investment of cement, which passes over the enamel in front of the tooth as well as covering its back and sides. They are unlike the teeth of other marsupials in their structure, as the dentinal tubes do not penetrate the enamel, which is, therefore, probably harder and denser and so less readily worn away.

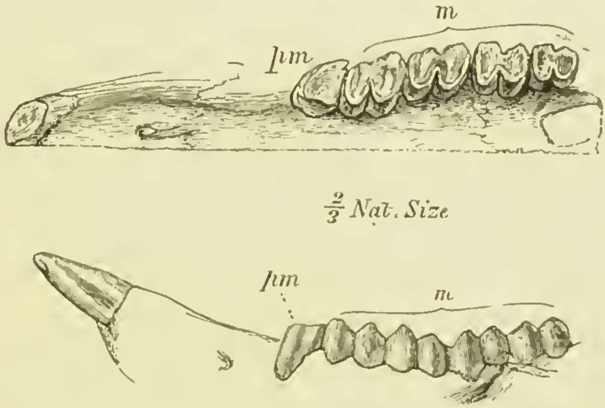
The molar teeth also grow from persistent pulps, and are very deeply grooved upon their sides, so that their grinding surfaces are uneven.

Their dental formula is —

$$i\,\frac{1}{1}\ c\,\frac{0}{0}\ p\,\frac{1}{1}\ m\,\frac{4}{4}.$$

The first tooth of the molar series is a single column, whereas the deep grooving of the others divides them into two columns, so that its simpler appearance, as well as analogy, would indicate that it is a premolar.

Fig. 272 ([1]).



The adaptive resemblance to the dentition of the true rodents is exceedingly close, though the Wombat is an undoubted marsupial ; and the very closeness of the imitation is an exemplification of the fact that adaptive characters are very apt to mislead, if used for the purposes of classification.

Extinct Wombats, of very much larger size than the recent species, are found in the later Tertiary deposits of Australia.

Another peculiarity of the Wombats has been described by Röse, who confirms a long-discredited statement of Owen's, that deciduous teeth were found in it, and says that the Wombat has two dentitions, altogether like a placental mammal.

([1]) Upper and lower teeth of Wombat (Phascolomys wombat).

He finds that there are calcified predecessors to the functional incisors, a deciduous canine which has no successor, and a deciduous premolar; all of these appear to be absorbed or shed at a very early period.

Amongst the marsupials there is a pretty little arboreal creature (Tarsipes), not larger than a small rat, which subsists upon insects and the nectar of flowers, which it reaches by means of a long protrusible tongue. Its molar teeth are rudimentary, variable in number, and are soon shed; the lower incisors, which are procumbent, are, however, retained, as are a few small teeth which are opposed to them above.

Another remarkable South American marsupial was described by R. F. Tomes, 1863, under the name of Hyracodon, but this name being already occupied, it is now termed Cœnolestes. (Thomas, "Proc. Zool. Soc.," 1895.)

Its dental formula is—

$$i\,\frac{4}{3}\;c\,\frac{1}{1}\;pm\,\frac{3}{3}\;m\,\frac{4}{4}.$$

It is remarkable as, though a true marsupial, it differs widely from the other American marsupials, and resembles those of Australia; the Diprotodonts have a syndactyle foot (*i.e.*, two toes contained in one skin), while among Polyprotodonts the Peramelidæ have the syndactyle foot, but are not diprotodonts; and American opossums are not diprotodont nor have they the syndactyle foot.

Cœnolestes, however, has much of the diprotodont character in its dentition and yet has not the syndactyle foot, so that it crosses the usual lines of classification and blends the characters of several groups.

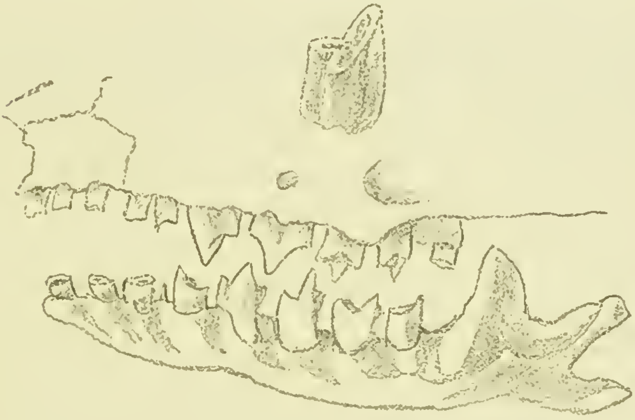
Its upper incisors are not unlike those of Didelphys, and it has a well-developed canine, but its lower incisors have the front pair much elongated, as in Diprotodonts.

The premolars are compressed cutting teeth, the last being much the largest. The upper molars are low-crowned and squarish, the first two having four cusps, the third three, and the last being a minute triangular tooth.

In the lower jaw, behind the big procumbent incisor, come four minute teeth, probably two incisors, a canine, and one premolar: the other two premolars are narrow sharp teeth, and the lower molars are elongated from before backwards, and more or less ovate in general form.

Within the last few years Mr. Ed. Stirling has discovered a marsupial mole, to which the name **Notoryctes** has been given. By Mr. Stirling's kindness I have had the opportunity of examining the structure of its teeth, and have found ("Proc. Zool. Soc.," 1897) that it presents the usual marsupial character of penetration of the enamel by tubes continuous with those of the dentine, the pattern being like that of Didelphyidæ. Its teeth, at first pointed like those of an insectivorous animal, become worn down, probably by the sand in which it lives and which it takes in with its food, so that they present areas of dentine surrounded by an upstanding ring of enamel, more or less elevated in places.

FIG. 273 (¹).



The feeble implantation of its teeth points to its food not being really hard, and it appears to live upon larvæ.

The wonderful diversity of the forms into which the marsupials have branched out in Australia seems to prove that they have been established in that region, and have

---

(¹) Upper and lower teeth of Notoryctes (× 4). The worn surface of a lower molar is shown yet more magnified in the single tooth placed above.

been without the competition of more highly organised placental mammals, for a prodigious length of time; and one cannot better conclude the very brief survey of the teeth of mammalia which has been attempted in this volume than by calling the reader's attention again to the character of the marsupial fauna—this microcosm, in which every place is filled by a marsupial which mimics the placental mammal which it represents—for nowhere can we more plainly see the workings of natural selection than in areas thus isolated and deprived of immigrant creatures for countless ages.

APPENDIX.

In the section of this book which treats of the enamel of elasmobranch fishes (p. 33) some doubt was expressed as to the point whether the outer hard layers of these teeth were to be rightly described as enamel at all.

Since those pages were finally corrected I have myself been working at this subject, and a paper bearing upon it (Röse, "Anat. Anzeig.," October, 1897) has come to my notice. Röse comes to the conclusion that it is not enamel, but a tubular dentine coated with—in places, at all events—a very thin layer of vitro-dentine; but my own investigations have led me to a totally different interpretation.

For, whatever it may be, it certainly is sharply marked off from any known dentine; its manner of calcification is totally different, and the differences can be seen in any section of the developing teeth of *Carcharias*, where true fine-tubed dentine is being developed immediately under this layer, but not in it.

A summary of my views will be found in the Royal Society's Proceedings for February, 1898; they are briefly as follows:

The so-called enamel differs absolutely from any known dentine in that, when decalcified, it disappears *in toto*, leaving but a minute formless residue; there is no collagen basis which takes stains strongly during its development, as in all dentines and in bone, and in its optical, physical and chemical characters it resembles enamel rather than dentine.

But, on the other hand, it has real differences from any other known enamel, for the organic matrix in which it is calcified is beyond question laid down by the outer part of the dentine papilla. *Primâ facie* this might seem to settle the question in favour of its being a dentine, though a perfectly anomalous one; but, just at the period that this layer of the dentine papilla is at its maximum, the ameloblasts suddenly attain to an enormous size. Over the next younger tooth they are small, and over the next older tooth they have again dropped down to a small size, have lost their distinctness of outline, and have otherwise changed.

Without entering into detail, it seems obvious that they have a short period of great activity, after which they are spent, and the only plausible explanation would seem to be that they are concerned in the calcification of this peculiar layer, for it is just at this period that it does calcify. If this view is correct, then the elasmobranch fish, just as they show us the first introduction of specialised teeth, present the first differentiation of enamel as a separate tissue, in the form of a joint product of the epiblastic enamel cells and the mesoblastic dentine papilla; afterwards, as tooth development came to be a slower and more deliberate process, as happens in many other fish and in reptiles and mammals, the ameloblasts took upon themselves the whole work.

Röse's paper, to which I have alluded, attempts a comprehensive classification of all calcified tissues, and in so doing he proposes a slightly different classification of dentines from that to be found in these pages. (Cf. p. 81.)

He does not admit plici-dentine into the list, and proposes the term trabecular-dentine instead of my osteo-dentine, my plici-dentines being for the most part or entirely relegated to this group of dentines. However, I do not agree with the conclusions which he has drawn; and, although the classification of dentines is avowedly not quite satisfactory, I do not think that proposed by Röse materially improves the position; for, when tested by actual application, it seems to me to break down, and to lead to more inconsistencies than the old one; the general question, however, is too large for discussion here, and my reasons for not accepting his conclusions will be found elsewhere. ("Anat. Anzeig.," 1898.)

INDEX.

A.

PAGE
Aard-Vark 374
Aardwolf 469
Absorption of teeth . . . 217
Acquired characters, inheritance of 322
Adaptive modification 309, 314
Adder 279
Æluroidea 459, 466
Acrodont teeth 273
Age, as determinable by teeth development 139
Aglypha 277
Albrecht, on intermaxillary bone 531
Allotheria 328
Alveolar arches, growth of 209, 212, 217
Alveolar process 546
Alveoli, nature of 546
Alveolo-dental membrane . . 104
Amblypoda 440
Ameloblasts . . 168, 121, 160
,, atrophy of 163, 586
Amphilestes 331
Amphicyon 464
Amphioxus 236
Amphitherium 328
Anarrhicas 254
Anchylosis, attachment by 228, 235
Anchitherium 412
Andrews, views on enamel development . . 164, 170
Angle, facial 517
Angler, the 253
Anomodont reptiles, no succession in 153
,, ,, teeth of . 289
Anoplotherium, dentition of 399
Ant-eaters 371
Anthropidæ 516

PAGE
Antrum, anatomy of . . 548
Apes, comparison of teeth with man 515
Apes, variability in . . . 515
Archæopteryx 294
Archetype theory . . . 308
Arctoidea 459, 472
Armadillo, succession in . . 356
Articulation, temporo-maxillary 553
Articulation of the teeth . 528
Artiodactyle ungulata . . 392
Ateles 506
Attachment of teeth . . . 222
Attachment by fibrous membrane 222
Attachment by elastic hinge . 223
,, ,, anchylosis . . 228
,, bone of . . 229
,, on pedestals . 231
,, by sockets 232, 234
Aye-Aye, teeth of . . 314, 503

B.

Babirussa, teeth of . . 397
Baboons, ,, . . . 506
Balænidæ 383
Barracuda, pike 261
Basal layer of Weil . . . 90
Basement membrane . 124, 137
Bathysaurus 227
Batrachia 265
Bats 495
Bdellostoma 237
Bears 473
Beaver, enamel of . . . 16
Beluga 375
Bettongia 577
Bicuspids of man 536
Bilophodont, meaning of . . 408
Binturong 467
Birds, teeth of 293

PAGE
Black, on lime salts of teeth . 41
Blind worm 273
Bödecker, on enamel . . . 18
,, on dentine . 54, 61
Boll, on nerves of pulp . . 89
Bone of attachment . . 229
development of . . 230
method of modelling . 115
Bonwill, triangle theory of . 529
Bovidæ 407
Brachydont, meaning of . 391
Bradypus . . . 371, 373
Branchial arches . . . 195
,, ,, teeth on . 244
Brontotheridæ 422
Brown striæ of Retzius . . 26
Buccinator 551
Buccal cavity, primitive . 195
Bunodont, meaning of . . 391
Bungarus 278
Bunotheria 448

C.

Calamodon 375
Calcification 154
,, by conversion . 160
,, by excretion 154, 159
,, of cementum . 190
,, of dentine . . 174
,, of enamel . . 159
,, of osteo-dentine . 189
,, of vaso-dentine . 186
Calcoglobulin 157
,, in ameloblasts . 160
Calcospherites 155
Camel 401
Camper, facial angle of . . 517
Canaliculi of cementum . . 93
Canidæ 464
Canines, definition of . . 348
,, homologies of 348, 483
,, of man 535
,, sexual development of 317
,, sexual development of, in horse . . 421
,, sexual development of, in deer . . 403
,, sexual development of, in monkeys . 508
Capybara, molars of . 451, 453
Carcharias 243
Carnassial teeth . 460, 462

PAGE
Carnivora 459
Cartilage, interarticular . . 553
Castration, effect of, on tusks . 393
Catarrhine monkeys . . 505
Cebidæ 505
Cementum, structure of . . 92
,, matrix of . . 93
,, calcification of . 190
,, development of . 134
,, organ . . . 134
Centetes 489
Centres of ossification of jaws . 196
Ceratodus 264
Cervidæ 403
Cestracionts 244
,, (?) enamel of . 35
Cetacea 375
,, milk teeth of 375, 383
,, dentine of . . . 376
Chætodonts 248
Chamæleon 272
,, absence of succession in . . . 151
Chauliodus 292
Chelonia 267
Chevrotain 403
Chimpanzee 514
Chin, absence in apes, &c. . 550
Chiromys . . . 314, 503
Chiroptera 495
Cholœpus 373
Chrysochloris, molars of . 493
Ciliiform teeth 249
Cingulum, nature of 468, 532, 535
,, theory of cusps 337, 346
Classification of teeth . . 347
Cleft palate 531
Coatimundi 473
Cobra 279
Cod, dentine of 72
Cœnolestes 581
Collagen . . . 39, 177, 181
Colubrine snakes . . . 277
Concomitant variation . . 318
Condylarthra 443
Connective tissue, theory of dentine development . . 177
Contour lines of Owen . . 45
Cope, doctrine of Kinetogenesis 322
,, ,, Trituberculism 331
Coronoid process, share of in growth of jaws . . . 208
Correlations of growth . . 318
Crait 278

PAGE
Craspedocephalus . . . 280
Creodonts 459
Crocodile 268
,, implantation of teeth 269
Crypts of developing teeth . 200
Ctenacodon 329
Cusps, development of . . 129
,, homologies of . . 401
,, modifications of . 338, 343
,, theories of formation of 322, 326
Cuticula dentis 97
Cyclostomata 236
Cynodraco 292
Cynognathus 290
Cynoidea 459, 464
Cystophora 478
Czermak, interglobular spaces of 58

D.

Dasypeltis 277
Dasypus 371
Dasyurus . . . 564, 574
Deer, sexual canines of . . 403
Deficiency of teeth in hairy men . 319
,, ,, in hairless dogs . 319
Dental furrow 126
,, formula 353
,, follicle 130
,, index 526
Dentinal fibrils 50
,, sheaths 47
,, tubes 44
Dentine, calcification of . . 174
,, classification of . 81
,, chemical composition of 39
,, connective tissue in . 177
,, distribution of . 8, 38
,, fibrils of 50
,, sheaths of . . . 47
,, tubes of 44
,, matrix of . . 39, 43
,, globular . . 60, 183
,, granular layer of . 58
,, lamination of . . 182
,, rate of growth of . 184
,, secondary . . . 83
,, sensitiveness of . 57
,, varieties of . 81, 586

PAGE
Dentine, theories of formation of . . . 177, 185
Dentine papilla 112, 123, 129
Dentition, milk 356
,, post-permanent 361, 369
,, premilk . 312, 369
,, typical mammalian 353
Dents en velours, en brosse, &c. 249
Dermal spines, relation to teeth . . 3, 112, 143, 262
Desmodus 496
Development of the teeth . . 110
,, in fish . . 236
,, in reptiles . . 265
,, in mammals . 113
,, of dentine 129, 174
,, of cementum . 190
,, of enamel . . 160
,, of the jaws . . 195
,, of alveoli . . 209
,, of bone of attachment . . 229
,, of early germs . 111
Diastema, the 459
Diademodon 292
Dingo 465
Dinoceras 441
Dinosauria 287
Dinotherium 435
Diodon 255
Diphyodonts 356
Diprotodonts . . . 327, 572
Dog 464
Dog-fish 3, 144
Dolphin 376
Dugong 386

E.

Echidna . . . 300, 305
Ebner, Von, on enamel 19, 21, 27
,, on bone . . 43
Edentata 370
Eel 232
Elachistodon 277
Elaphodus 404
Elasmobranch fish . 142, 585
Elastin 39
Elephant, tusks of . 424, 428
,, molars of . 343, 437
,, succession of teeth in 434
,, milk teeth of 421, 434
Eminentia articularis . . 553
Enamel, calcification of . . 159

PAGE
Enamel, cavities in 27
,, chemical constitution 11
,, development of 164
,, ,, of tubular 164
,, distribution of 8, 13, 146
,, marsupial 29
,, pigmentation of 450
,, prisms of 14, 20, 26
,, structure of 14
,, tubular 29, 456, 495
,, theories as to formation 171
,, organ, as form-builder 107, 128
,, ,, origin of 121
,, ,, neck of 122
,, ,, stages of 117, 119
,, ,, vascularity of 127
,, ,, universality of 129
Encapsuled lacunæ 94
Endognathion 197
Eocene mammals 328
Eohippus 413
Epiblast 2, 195
Equus 416
Erinaceus 485
Eruption of teeth 211
,, dates of 213
,, influence of nutrition on 321
Esthonyx 446
Eupleres 468
Eutheria, ancestry of 306
Evolution of tooth forms 325
External pterygoid muscle, action of 555

F.

Face, formed by maxillæ 558
Facial angle 517
Feeding, effects of, on development of teeth 320
Felidæ 469
,, ancestry of 471
Fibrils, dentinal 50
Fish, teeth of 236
Flounder, dentine of 73
Fœtus (nine months), jaws of 198
Follicle, dental 133
Foregut 195
Formula, dental 353
Frog 265
,, development of teeth of 150

G.

PAGE
Gadidæ 254
Galeopithecus 483
Galippe, Dr., percentage of lime salts in teeth 41
Ganoid fish 248
Ganodonta 375
Gelatine 39
Germ, tooth 110
Gibbons 508
Glands, of Serres 103
,, salivary 558
Glenoid cavity 453, 553, 556
Globiocephalus 375
Globular dentine 60
Glyptodon 374
Gnathic index 519
Gomphosis 234
Goodsir, views of 136
Gorilla 508
Grampus 377
Granular layer of dentine 58
Gubernaculum 135
Guinea-pig 457
Gum, structure of 103
Gymnodonts 255
Gymnura 488

H.

Haddock, teeth of 232
Hair, abnormalities in teeth and 319
Hake, dentine of 68
,, hinged teeth of 71
Halicore 386
Halmaturus 577
Haplodont, meaning of 336
Hare 449
Hare lip 531
Harting, researches on calcification 157
Hatteria 151, 273
Hedgehog 360, 485
Heitzmann, on cementum 95
Heloderma 272
Hemiganus 375
Hesperornis 296
Heterodont, meaning of 356
Hinged teeth 250, 253
Hipparion 415
Hippocampus 260
Hippopotamus 398
Homalodontotherium 421

PAGE

Homodonts . . . 326, 356
Homologies of the teeth 3, 347
,, of marsupial teeth 364
,, of milk dentitions 358, 368
,, of the molars . 367
Hoppe-Seyler, analyses of enamel . 41
,, analyses of dentine . 41
,, bone salt of 41, 159
Horny teeth 237, 301
Horse, incisors of . . . 339
,, evolution of molars of 411, 413, 420
,, teeth a test of age . 418
,, ancestry of . . . 413
Howship, lacunæ of . . 217
Huxley, views on development 137
Hyæna 467
Hyænodon 461
Hydromys 449
Hydrophis 278
Hydropotes 405
Hylobates 508
Hyperoodon 378
Hypoblast 2, 195
Hypocone 332
Hypsiprymnus 576
Hypsodont . . . 391, 415
Hyracodon 421
Hyracotherium 412
Hyrax 422
Hystrix 17, 458

I.

Ichneumon 466
Ichthyornis 296
Ichthyosaurus 270
Iguana 272
Iguanodon 288
Incisors, definition of . . 347
,, human 531
,, missing of man . . 531
Indri 501
Inferior dental canal . . . 552
Inheritance of acquired characters 322
Insectivora 481
,, cusp patterns of 340, 493
,, molars of . . . 493

PAGE

Interglobular spaces . . . 58
Intermaxillary bone . . . 147
Interarticular cartilage . 555, 557
Internal epithelium of enamel organs 160
Internal pterygoid muscle . . 554
Ivory 426

J.

Jaws, at birth 198
,, at seven years . . . 206
,, adult and old age . . 206
,, centres of ossification . 196
,, arrested growth of . 209
,, muscles of . . . 554
,, variation in size of . . 526

K.

Kangaroo 578
Kinetogenesis . . . 322, 503
Klein, on structure of enamel . 19
,, ,, dentine . 56

L.

Labyrinthodon 267
,, dentine of . . 65
Lamprey 6, 237
Lamna 240
,, dentine of . . . 79
,, enamel of . . 32, 585
Lacunæ, development of . . 192
,, encapsuled . . 94
,, of cementum . . 93
Leche, on development of teeth 114, 119
,, on premilk teeth 362, 365
,, on milk teeth of insectivora . . 485
Lemurs 500
Lepidosiren 262
Lepidosteus, dentine of . . 62
Lepidotus, enamel of . . . 31
Leporidæ 456
Ligaments, of jaw . . . 553
Lines of Schreger . . . 27, 45
Lippenfurche 114
Lizards 270
Lophodont 408
Lymphatics, absence of in pulp 88
,, supposed in root membrane 107, 128, 561

M.

PAGE
Macacus 506
Machairodus 470
Mackerel 233
Macropus 578
Macroscelis 483
Magitot, on dentine . . . 56
,, on cement organ . 134
,, on odontoblasts and nerves 57
Malassez, on epithelial rests . 128
,, on alveolo-dental membrane 128
Mammals, classification of . . 299
,, ancestry of . 292, 300
,, typical dentition of 353
Mammoth, tusks of . . . 426
Man, dentition of . . . 516
,, teeth of races of . 517, 523
,, palæolithic . . 517, 519
Mandible, description of . . 550
Manatee, teeth of . . . 388
,, dentine of . . . 75
Manis, tooth rudiments of . 370
Mark of horses' incisors . . 417
Marmosets 507
Marsupials 562
,, change of tooth in 565, 569
,, homologies of functional teeth . . 364
,, enamel of . . 28
Mastication, motions of . . 555
Mastodon 433
,, molars of . . . 344
Matrix of bone 39
,, of cementum . . . 39
,, of dentine . . 39, 43
,, of enamel . . . 10
Maxillary bones, anatomy of . 545
,, development of . 195
Mechanical theory of tooth forms 322
Meckel's cartilage . 113, 196
Megaderma 498
Megadonts 527
Megatherium 73
Melursus 475
Membrana eboris . . 87, 130
,, preformativa . 164, 137
,, alveolo-dental . 104
Mental foramen 203
Merganser, bill of . . . 291
Mesoblast 2
Mesodont 507
Mesognathion 519
Mesonyx 482
Mesoplodon 379
Mesotherium 445
Mesozoic mammals . . . 327
Metacone 332
Metatheria 299
Microdont 527
Microlestes 304
Milk dentitions . 356 *et passim*
,, absence of . . 369
,, origin of supposed . 368
,, of marsupials . 563
Miohippus 413
Molars, definition of . . 347
,, of man . 367, 523, 540
,, homologies of . . 484
Mole, teeth of 491
,, marsupial . . . 582
Monitor 271
Monkeys, Catarrhine . . . 506
,, Platyrrhine . . 505
Monodon 381
Monophyodonts . . 326, 356
Monotremata 300
Moschus 405
Mouth, development of 3, 195
Multituberculata . . . 328
Mummery, on dentine development . . . 177
,, on nerves of pulp . 58
Muscles of jaw 554
Musk deer, canines of . 317, 405
Mustelidæ 472
Mycetes 506
Myliobates, dentine of . . 67
,, teeth of . . . 247
Myrmecobius . 364, 563, 573
Myrmecophaga 370
Mystacoceti 383
Myxine 7, 237

N.

Narwal 381
Nasmyth's membrane . . 97
Naso-frontal process . . 197
Nasua 473
Natural selection, theory of . 310
Nerves, of pulp . . . 55, 88
,, of the teeth . . 559

PAGE
Nerves, fifth 559
Neumann, sheaths of . . 40, 47
Newt 149
Notoryctes 581

O.

Oblique ridge, of human molars
Odontoblasts . . 56, 87, 175
Odontopteryx 294
Odontornithes 293
Odontostomus, hinged teeth of 227
Ophidia . . . 151, 277
Opisthoglypha 277
Opossum 574
Orang 510
Oreodon . . . 348, 401
Ornithorhyncus . . . 300
Ornithosauria 267
Orthognathism 519
Orycteropus . . . 371, 374
Osseous fish, teeth of . . 248
Ossification, centres of in jaws 196
Osteoblasts 191
Osteoclasts 217
Osteo-dentine . . 76, 189
Ostracion, dentine of . . 68
Otaria, erosion of teeth in . . 476
Otocyon . . . 464, 466

P.

Palæotherium 410
Pantotheria 327
Paul, on Nasmyth's membrane 31, 97
Paracone 332
Paradoxurus 467
Papilla, dentinal . . 112, 123
Parrot fish 257
Perameles 568
Periosteum, alveolo-dental . 104
Perissodactyle ungulata . . 407
Permanent teeth, eruption of . 211
,, development of 116, 361
Petrogale . . . 565, 567
Phacochœrus 395
Phalangers 574
Pharyngeal teeth . . . 260
Phascolarctos 575
Phascolomys 580
Phenacodus . . . 391, 443
Phoca 477
Phocœna 376
Physeter 378

PAGE
Phyllodus 263
Pig 392
Pike, dentine of . . . 79
,, teeth of . . . 250
Pithecidæ 506
Plagiaulax 329
Platurus 278
Pleurodont 271
Pleuronectidæ, dentine of . . 71
Plici-dentine 62
Pliohippus 414
Poison fangs 281
Polymastodon 330
Polyprotodonts . . 327, 572
Porcupine, enamel of . . . 17
Post-permanent dentition, supposed . 361, 369, 577
Precanine 531
Premilk dentition, supposed 362, 369, 567
Premolars, definition of . . 348
,, of man . . . 536
,, forms of in higher life . . . 571
,, order of loss of . . 474
,, homologies of first 353, 393, 398, 401, 407, 409, 464, 477 *et passim*
Primates 500
Primitive buccal-cavity . . 195
Primitive triangle (Trigon) . 333
Priodon 373
Pristis 246
Proboscidea 424
Processus globulares . . 197
Procyonidæ . . 459, 472
Prognathism . . 210, 513, 520
Proteles 468
Proteroglypha 277
Protocone 336
Protodont 332
Prototheria 300
Pseudoscarus 258
Psittacotherium 375
Pteranodon 293
Pterodactyles 293
Pteromyzon 237
Pteropus 293
Pterosauria 497
Puerco mammals . . . 328
,, edentates . . . 375
Puff adder 279
Pulp, structure of 86
Python 272

R.

PAGE
Rachiodon 277
Rainie, researches on calcification 155
Rat 451, 458
Rays 247
Reptiles, teeth of 265
,, ,, for breaking egg 267
,, development of teeth 148
Retzius, brown striæ of . . . 26
Rhinoceros 409
Rhinolophus 498
Rhyncocephalus 273
Rhytina, dentition of . . 389
Rodentia 448
,, milk dentition of . 456
Rodents, ancestry of . . 316
,, enamel of . . . 455
,, food of 451
,, molars . . . 451
,, extinct 458
Root membrane 104
Röse, on dentinal sheaths . 50
,, on tooth germs . . . 115
,, on premilk and post-permanent teeth . 362, 369
,, on enamel development . 171
Rostral teeth 246
Rudimentary teeth 309, 369, 375, 378, 386, 388 *et passim*
,, milk teeth 457, 358, 360
,, tooth germs . . 360
Ruminants 403
,, absence of incisors in 403
,, milk teeth of . . 403

S.

Salmon 261
Salivary glands 558
Sargus 260
,, enamel of . . . 36
Saurians 270
Saw-fish 246
Scales of dogfish 3
,, Lepidosteus . . . 4
Scalpriform incisors . . . 449
Scarus 257
Schreger, lines of in enamel . 27
,, ,, dentine . 45
Seals 475
,, milk dentition of . . 475
Secondary dentine . . . 83

PAGE
Secondary dentine in rodents . 453
Selache 244
Selachia, teeth of . . . 240
Selenodont teeth . . . 391
Serres, glands of . . 122, 103
Setiform teeth 249
Sexual weapons, teeth used as 317
,, differences in teeth of . 405
,, ,, cervidæ . . 379
,, ,, cetacea . 379
,, ,, dinotherium 436
,, ,, elephant 425, 428
,, ,, horse . . 421
,, ,, protoceras . 443
,, ,, monkeys 508, 514
,, ,, sirenia . 386
Sharpey's fibres . . 95, 105
,, ,, in osteo-dentine 190
Sharks, teeth of . . . 240
Sheep's-head fish . . . 257
Sheaths of Neumann . . . 47
Shrew 489
Shrews, milk teeth of . . 369
Siluroids 249
Sirenia, teeth of . . . 385
Simia 510
Simiadæ 505
Sloth, teeth of . . . 373
Smilodon . . . 470, 471
Snakes, development of teeth in 151
Socketed implantation of teeth 234
Sorex 489
Stages of tooth germs . . 139
,, at various ages . . 140
Stellate reticulum . 120, 125
Stomodæum . . . 3, 197
Stratum intermedium . . 121
Sturgeon 260
Sperm whale 378
Spee, Von, globules of . 162, 172
Sphenodon 273
Sphyræna 261
Squalodon 375
Succession of teeth in sharks . 243
,, ,, in mammals 361
,, in proboscidea . . 433
Sword-fish 249
Sus babirussa, dentition of . 397

T.

Tadpole, horny jaws of . . 266
Talon, the . . . 333, 495
Talpa 491

PAGE
Tapir 408
Tarsipes 581
Tatusia 371
Taxeopoda 422
Teeth, calcified 8
,, horny . . . 1, 5, 7, 237
,, homologies with dermal spines 2
,, classification of . . . 347
,, dates of eruption . . . 213
,, as tests of age . . . 321
,, tables of stages of tooth germs at various ages 139
Teething 211
Teleostei, tooth germs of . . 146
Temporal muscle 557
Tenrec 489
Tetralophodon 408
Tetrodon 257
Thylacine 572
Thylacoleo 577
Tiger 460
Tillodonts 445
Tillotherium 447
Tinoceras 442
Tissues, dental 8
Tomes' processes of ameloblasts 160, 164
,, fibrils 50
Tooth band 113
,, definition of . . . 1
,, germs (early) 110
,, ,, at various ages . 139
,, ,, forms, genesis of 308
Topinard, on molars of man . 523
Tortoises 267
Toxodon 444
Trabecular-dentine . . . 586
Tragulina 403
Trichechus 478
Triconodon 336, 566
Triangle, Dr. Bonwill's theory 529
,, primitive . . . 333
Trigon 333, 487
Tritubercular teeth 327
,, in insectivora 482, 487
,, lemurs . . . 501
Trituberculism, theory of . . 331
,, difficulties in accepting . 458, 336, 487, 494
Tuberculo-sectorial teeth . 333
Tubular enamels 170
Tusks of elephant 428
,, of wild boars . . . 394

U.

PAGE
Ungulata 390
,, early forms of . . 391
,, artiodactyle . . 392
,, perissodactyle . . 407
,, molar patterns of 342, 410
Urotrichus 494
Ursus 474

V.

Vampire 496
Varanus 271
,, dentine of 62
Variation in teeth . . . 312
,, causes of . . 32
Variability in monkeys' teeth . 515
Vascular canals, in human dentine . 74
,, ,, in dentine of Sargus . 75
,, ,, in dentine of manatee 76
Vaso-dentine 68
,, development of . 186
Vestibulum oris 114
Villiform teeth 249
Vipers 280
Visceral arches 195
Viverra 466

W.

Walrus 478
Wart-hog 395
Weil, basal layer of . . . 90
Whalebone 384
Whales 375
Williams, Leon, on enamel 22, 24
,, development . 164, 171
,, on membrana preformativa . 139
Wisdom teeth in man and apes 516
,, in man . . 522
,, date of eruption in apes 509
Wolf-fish 254
Wombat 568, 579
Woodhead, Sims, on calcification 158
Woodward, homologies of teeth 353
,, on milk dentition 360, 365

	PAGE
Woodward on milk teeth of insectivora	487
Wrasse	261
Wilson and Hill, on marsupial succession	363

Z.

	PAGE
Zahnleiste	113
Zahnwall	115
Zeuglodon	375
Ziphoid cetaceans	378

THE END.

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Allen's Chemistry of Urine, 22
——— Commercial Organic Analysis, 26
Anderson on Fingers and Toes, 18
Armatage's Veterinary Pocket Remembrancer, 28
Barnes' (R.) Obstetric Operations, 6
——— Diseases of Women, 6
Beale (L. S.) on Liver, 12
——— Microscope in Medicine, 12
——— Slight Ailments, 12
——— Urinary and Renal Derangements, 22
Beale (P. T. B.) on Elementary Biology, 3
Beasley's Book of Prescriptions, 8
——— Druggist's General Receipt Book, 8
——— Pocket Formulary, 8
Bell on Sterility, 6
Bellamy's Surgical Anatomy, 2
Bentley and Trimen's Medicinal Plants, 9
Bentley's Systematic Botany, 9
Berkart's Bronchial Asthma, 13
Bernard on Stammering, 14
Bernays' Notes on Analytical Chemistry, 26
Bigg's Short Manual of Orthopædy, 18
Bloxam's Chemistry, 25
——— Laboratory Teaching, 25
Bousfield's Photo-Micrography, 28
Bowlby's Injuries and Diseases of Nerves, 17
——— Surgical Pathology and Morbid Anatomy, 17
Brockbank on Gallstones, 15
Brodhurst's Anchylosis, 17
——— Curvatures of Spine, 17
——— Talipes Equino-Varus, 17
——— Congenital Dislocation of the Hip, 17
Brown's Practical Chemistry, 26
Bryant's Practice of Surgery, 17
Burckhardt and Fenwick's Atlas of Electric Cystoscopy, 22
Burdett's Hospitals and Asylums of the World, 4
Butler-Smythe's Ovariotomies, 6
Butlin's Malignant Disease of the Larynx, 21
——— Operative Surgery of Malignant Disease, 21
——— Sarcoma and Carcinoma, 21
Buzzard's Diseases of the Nervous System, 14
——— Peripheral Neuritis, 14
——— Simulation of Hysteria, 14
Cameron's Oils, Resins, and Varnishes, 27
——— Soaps and Candles, 27
Carpenter aud Dallinger on the Microscope, 28
Carpenter's Human Physiology, 3
Cautley on Feeding Infants, 7
Charteris on Health Resorts, 15
——— Practice of Medicine, 11
Chauveau's Comparative Anatomy, 28
Chevers' Diseases of India, 10
Churchill's Face and Foot Deformities, 18
Clarke's Eyestrain, 19
Clouston's Lectures on Mental Diseases, 4
Clowes and Coleman's Quantitative Analysis, 25
Clowes and Coleman's Elementary Practical Chemistry, 25
Clowes' Practical Chemistry, 25
Cooley's Cyclopædia of Practical Receipts, 27
Cooper's Syphilis, 23
Cooper and Edwards' Diseases of the Rectum, 24
Cripps' (H.) Cancer of the Rectum, 24
——— Diseases of the Rectum and Anus, 24
——— Air and Fæces in Urethra, 24
Cripps' (R. A.) Galenic Pharmacy, 8
Cuff's Lectures to Nurses, 7
Cullingworth's Manual of Nursing, 7
——— Monthly Nurses, 7
Dalby's Diseases and Injuries of the Ear, 20
———Short Contributions, 20

[*Continued on next page.*

Day on Diseases of Children, 7
—— on Headaches, 15
Domville's Manual for Nurses, 7
Doran's Gynæcological Operations, 6
Druitt's Surgeon's Vade-Mecum, 17
Duncan (A.) on Prevention of Diseases in Tropics, 10
Ellis's (E.) Diseases of Children, 7
Ellis's (T. S.) Human Foot, 18
Fagge's Principles and Practice of Medicine, 10
Fayrer's Climate and Fevers of India, 10
—— Natural History, etc., of Cholera, 10
Fenwick (E. H.), Electric Illumination of Bladder, 22
—— Tumours of Bladder, 22
—— Symptoms of Urinary Disease, 22
Fenwick's (S.) Medical Diagnosis, 12
—— Obscure Diseases of the Abdomen, 12
—— Outlines of Medical Treatment, 12
—— The Saliva as a Test, 12
Fink's Operating for Cataract, 19
Flower's Diagrams of the Nerves, 2
Fowler's Dictionary of Practical Medicine, 11
Fox (Wilson), Atlas of Pathological Anatomy of the Lungs, 11
——Treatise on Diseases of the Lungs, 11
Frankland and Japp's Inorganic Chemistry, 26
Fraser's Operations on the Brain, 16
Fresenius' Qualitative Analysis, 25
—— Quantitative Analysis, 25
Galabin's Diseases of Women, 6
—— Manual of Midwifery, 5
Gardner's Bleaching, Dyeing, and Calico Printing, 27
—— Brewing, Distilling, and Wine Manufacture, 27
Gimlette's Myxœdema, 12
Glassington's Dental Materia Medica, 20
Godlee's Atlas of Human Anatomy, 1
Goodhart's Diseases of Children, 7
Gowers' Diagnosis of Brain Disease, 13
—— Diseases of Nervous System, 13
—— Medical Ophthalmoscopy, 13
—— Syphilis and the Nervous System, 13
Granville on Gout, 14
Green's Manual of Botany, 9
Groves and Thorp's Chemical Technology, 27
Guy's Hospital Reports, 11
Habershon's Diseases of the Abdomen, 15
Haig's Uric Acid, 13
Haig-Brown's Elementary Physiology, 3
Harley on Diseases of the Liver, 14
Harris's (V. D.) Diseases of Chest, 11
Harrison's Urinary Organs, 23
Hartridge's Refraction of the Eye, 19
—— Ophthalmoscope, 19
Hawthorne's Galenical Preparations, 8
Heath's Certain Diseases of the Jaws, 16
—— Clinical Lectures on Surgical Subjects, 16
—— Injuries and Diseases of the Jaws, 16
—— Minor Surgery and Bandaging, 16
—— Operative Surgery, 16
—— Practical Anatomy, 1
—— Surgical Diagnosis, 16
Hellier's Notes on Gynæcological Nursing, 6
Higgens' Ophthalmic Out-patient Practice, 19
Hill on Cerebral Circulation, 3
Hillis' Leprosy in British Guiana, 20
Hirschfeld's Atlas of Central Nervous System, 2
Holden's Human Osteology, 1
—— Landmarks, 1
Hooper's Physicians' Vade-Mecum, 10
Hovell's Diseases of the Ear, 20
Hyde's Diseases of the Skin, 21
Hyslop's Mental Physiology, 5
Impey on Leprosy, 21

[*Continued on next page.*

Jacobson's Male Organs, 22
——— Operations of Surgery, 17
Jellett's Midwifery, 5
Jessop on the Eye, 18
Johnson's Asphyxia, 12
——— Cholera Controversy, 12
——— Granular Kidney, 12
——— Medical Lectures and Essays, 12
Journal of Mental Science, 5
Keyes' Genito-Urinary Organs and Syphilis, 23
Kohlrausch's Physical Measurements, 28
Lancereaux's Atlas of Pathological Anatomy, 2
Lane's Rheumatic Diseases, 14
Langdon-Down's Mental Affections of Childhood, 5
Lee's Microtomists' Vade-Mecum, 28
Lescher's Recent Materia Medica, 9
Lewis (Bevan) on the Human Brain, 2
Liebreich's Atlas of Ophthalmoscopy, 19
MacMunn's Clinical Chemistry of Urine, 22
Macnamara's Diseases and Refraction of the Eye, 18
——— Diseases of Bones and Joints, 17
McNeill's Isolation Hospitals, 4
Malcolm's Physiology of Death, 16
Mapother's Papers on Dermatology, 21
Marcet on Respiration, 3
Martin's Ambulance Lectures, 15
Maxwell's Terminologia Medica Polyglotta, 24
Maylard's Surgery of Alimentary Canal, 16
Mayne's Medical Vocabulary, 24
Mercier's Lunacy Law, 5
Microscopical Journal, 27
Mills and Rowan's Fuel and its Applications, 27
Moore's (N.) Pathological Anatomy of Diseases, 2
Moore's (Sir W. J.) Diseases of India, 10
Moore's (Sir W. J.) Family Medicine, etc., for India, 10
———Tropical Climates, 10
Morris's Human Anatomy, 1
Moullin's (Mansell) Surgery, 16
Nettleship's Diseases of the Eye, 18
Notter and Firth's Hygiene, 3
Ogle on Tympanites, 15
Oliver's Abdominal Tumours, 6
———Diseases of Women, 6
Ophthalmic (Royal London) Hospital Reports, 18
Ophthalmological Society's Transactions, 18
Ormerod's Diseases of the Nervous System, 13
Parkes' (E. A.) Practical Hygiene, 4
Parkes' (L. C.) Elements of Health, 4
Pavy's Carbohydrates, 12
Pereira's Selecta è Prescriptis, 8
Phillips' Materia Medica and Therapeutics, 8
Pitt-Lewis's Insane and the Law, 4
Pollock's Histology of the Eye and Eyelids, 19
Proctor's Practical Pharmacy, 8
Purcell on Cancer, 22
Pye-Smith's Diseases of the Skin, 21
Quinby's Notes on Dental Practice, 20
Ramsay's Elementary Systematic Chemistry, 26
——— Inorganic Chemistry, 26
Reynolds' Diseases of Women, 6
Richardson's Mechanical Dentistry, 20
Richmond on Antiseptics, 7
Roberts' (D. Lloyd) Practice of Midwifery, 5
Robinson's (Tom) Eczema, 21
——— Illustrations of Skin Diseases, 21
——— Syphilis, 21
Ross's Aphasia, 14
——— Diseases of the Nervous System, 14
Royle and Harley's Materia Medica, 9
St. Thomas's Hospital Reports, 11

[*Continued on next page.*

Sansom's Valvular Disease of the Heart, 13
Schweinitz on Diseases of the Eye, 19
Shaw's Diseases of the Eye, 19
Short Dictionary of Medical Terms, 24
Silk's Manual of Nitrous Oxide, 20
Smith's (E.) Clinical Studies, 7
———Disease in Children, 7
———Wasting Diseases of Infants and Children, 7
Smith's (J. Greig) Abdominal Surgery, 16
Smith's (Priestley) Glaucoma, 19
Snow's Cancers and the Cancer Process, 21
——— Palliative Treatment of Cancer, 21
——— Reappearance of Cancer, 21
Southall's Organic Materia Medica, 9
Squire's (P.) Companion to the Pharmacopœia, 8
———London Hospitals Pharmacopœias, 8
———Methods and Formulæ, 27
Starling's Elements of Human Physiology, 3
Sternberg's Bacteriology, 11
Stevenson and Murphy's Hygiene, 4
Sutton's (F.) Volumetric Analysis, 26
Sutton's (H. G.) Lectures on Pathology, 2
Sutton's (J.B.) General Pathology, 2
Swain's Surgical Emergencies, 15
Swayne's Obstetric Aphorisms, 5
Taylor's (A. S.) Medical Jurisprudence, 3
Taylor's (F.) Practice of Medicine, 10
Taylor's (J. C.) Canary Islands, 15
Thin's Cancerous Affections of the Skin, 22
——— Pathology and Treatment of Ringworm, 22
Thomas's Diseases of Women, 6
Thompson's (Sir H.) Calculous Diseases, 23
———Diseases of the Prostate, 23
———Diseases of the Urinary Organs, 23
Thompson's Introduction to Catalogue, 23
———Lithotomy and Lithotrity, 23
———Stricture of the Urethra, 23
———Suprapubic Operation, 23
———Surgery of the Urinary Organs, 23
———Tumours of the Bladder, 23
Thorne's Diseases of the Heart, 11
Thresh on Water Analysis, 4
Tilden's Chemistry, 25
Tomes' (C. S.) Dental Anatomy, 20
Tomes' (J. & C. S.) Dental Surgery, 20
Tooth's Spinal Cord, 14
Treves and Lang's German-English Dictionary, 24
Tuke's Dictionary of Psychological Medicine, 5
Tuson's Veterinary Pharmacopœia, 28
Valentin and Hodgkinson's Qualitative Chemical Analysis, 26
Vintras on the Mineral Waters, etc., of France, 15
Wagner's Chemical Technology, 7
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Waring's Indian Bazaar Medicines, 9
——— Practical Therapeutics, 9
Watts' Organic Chemistry, 25
West's (S.) How to Examine the Chest, 11
Westminster Hospital Reports, 11
White's (Hale) Materia Medica, Pharmacy, etc., 7
Wilks' Diseases of the Nervous System, 14
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———Surgery, 28
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